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Lake trophic status and bioaccumulation of polychlorinated biphenyls in benthic organisms: a comparison between littoral and profundal invertebrates

Niklas Holmqvist, Patrik Stenroth, Olof Berglund, Per Nyström, Wilhelm Graneli, and Per Larsson

Abstract: We investigated the influence of lake trophic status on accumulation of polychlorinated biphenyls (PCBs) in littoral and profundal invertebrates from 19 lakes in southern Sweden. The PCB concentration in profundal chironomids (*Chironomus* sp.) was negatively correlated with lake trophy but the concentration in littoral crayfish (*Pacifasticus leniusculus*) was unrelated to shifting nutrient regimes. PCB concentrations in chironomids were negatively correlated, while crayfish did not correlate with lake total phosphorus. Two findings indicate that different processes determine bioaccumulation in littoral and profundal invertebrates: (*i*) a lack of correlation between PCB concentrations in crayfish and chironomids within lakes and (*ii*) some differences in congener distribution in the two species. We suggest a possible explanation in that chironomids are directly exposed to settling material from the pelagic zone, while crayfish are omnivorous and feed mainly in the littoral zone. A intensive investigation on one pond population could not reveal any individual factors, such as lipid content, size, or sex, influencing bioaccumulation of PCBs in crayfish.

Résumé : Nous avons étudié l'influence du statut trophique du lac sur l'accumulation des biphényles polychlorés (BPC) par les invertébrés des zones littorale et profonde de 19 lacs du sud de la Suède. La concentration de BPC dans les chironomidés (*Chironomus* sp.) de la zone profonde est fonction négative du statut trophique du lac, alors que celle dans les écrevisses littorales (*Pacifasticus leniusculus*) n'a pas de relation avec les divers régimes d'éléments nutritifs. Les concentrations de BPC chez les chironomidés sont en corrélation négative avec le phosphore total du lac, alors que celles de l'écrevisse ne montrent aucune corrélation. Deux résultats indiquent que des processus différents déterminent la bioaccumulation chez les invertébrés des zones littorale et profonde: (*i*) l'absence de corrélation entre les concentrations de BPC chez l'écrevisse et le chironomidé dans un même lac et (*ii*) les différences dans la répartition des congénères des BPC chez les deux espèces. Nous suggérons comme explication que les chironomidés sont directement exposés aux particules qui précipitent depuis la zone pélagique, alors que les écrevisses omnivores se nourrissent surtout dans la zone littorale. Une recherche détaillée sur une population d'étang n'a pu révéler aucun facteur particulier, tel que le contenu lipidique, la taille ou le sexe, qui influence la bioaccumulation des BPC chez l'écrevisse.

[Traduit par la Rédaction]

Introduction

Eutrophication and accumulation of persistent pollutants in biota are two major environmental problems in European marine and freshwater ecosystems. Lately, some investigations have focused on interactions between these two processes. A negative relationship between lake trophic status and levels of polychlorinated biphenyls (PCBs) has been shown for different components of the pelagic food web, from phytoplankton to piscivorous fish (e.g., Taylor et al. 1991; Larsson et al. 1992; Kidd et al. 1999). Few studies have focused on the interaction between eutrophication and accumulation of persistent organic pollutants (POPs) in benthic animals. Benthic animals potentially bioaccumulate sediment-borne contaminants as they spend their life in intimate contact with the sediment. Gunnarsson et al. (2000) found in laboratory experiments that POP concentrations in benthic animals could, contrary to pelagic biota, increase with increasing trophic status of water bodies. Owing to increasing settling of organic-rich particles, the benthic bioactivity increases with increasing disturbance of the sediment (bioturbidation) (Gilek et al. 1996; Björk and Gilek 1997;

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Madsen et al. 1997). Bioturbation and increasing ventilation rates of sediments could enhance bioaccumulation of POPs in benthic invertebrates (Swackhamer and Skoglund 1993; Madsen et al. 1997; Gunnarsson et al. 2000).

The most commonly used explanation to the POP – lake trophy relationship in pelagic biota is that increased production or changes in the species composition of primary producers (phytoplankton), owing to excess of nutrients, cause a chain of events that results in reduced concentrations of POPs. The events include changes in the first link of the food chain where phytoplankton growth rate and lipid content affect bioconcentration of POP as well as increased sedimentation of organic matter (and POP) as a result of phytoplankton blooms. The growth dilution hypothesis is defined as the fast growth of phytoplankton, i.e., high cell division rates, that exceed uptake kinetics of POPs leading to decreasing concentrations in phytoplankton in nutrient-rich lakes (Taylor et al. 1991; Swackhamer and Skoglund 1993; Larsson et al. 2000). Alternatively, Berglund et al. (2001*b*) reported that decreasing concentrations of POPs with lake trophy is due to higher lipid content (and thus lipophilic POPs) in phytoplankton of oligotrophic systems owing to different species composition (mainly caused by diatom blooms) as a response to changing nutrient regimes.

Concentrations of various POPs in fish have been reported to follow the same pattern as in phytoplankton and decrease with increasing lake trophy. However, the explanation put forward was not a food chain related transport of pollutants dependent on growth rates or lipid content of phytoplankton. Instead, individual growth rate of fish was coupled to POP accumulation (Larsson et al. 1992): high nutrient status of the lake gives high growth rate of fish owing to high prey abundance leading to dilution of the pollutants following the same principle as for phytoplankton. Hence, by combining the different growth dilution events in plankton and at higher trophic levels, an additive effect of lake trophy in higher trophic levels within the pelagic food chain could be expected. However, Berglund et al. (2001*b*) could not find any such transport from phytoplankton to higher trophic levels (zooplankton and zooplanktivorous fish) within a lake trophy gradient.

The cycling of POPs in lakes is closely linked to the cycling of organic carbon. Organic carbon acts, owing to the lipophilic characters of POPs, as a major repository for POPs. Eutrophic lakes are characterized by large phytoplankton blooms that will increase the sedimentation of dead algae, organic carbon, when the blooms collapse (e.g., Larsson et al. 1998; Jeremiason et al. 1999). The total organic carbon mass in sediments will thus increase, by increased settling of dead algae, with increasing trophic status of lakes. The settling organic matter contains POPs that will accumulate in bottom sediments. This will lead to increased amounts of POPs in sediment but not necessarily increased concentrations. Lake morphometry affects the sedimentation process; in deep lakes, the major part of the organic carbon originating from phytoplankton is broken down, thereby concentrating POPs in sedimenting material (Larsson et al. 1998). The effect of lake trophic status on POP concentration in benthic biota is therefore not clear. Are high amounts of settling organic carbon and POPs in eutrophic lakes resulting in high levels of POPs in animals foraging in sediments or are processes in the pelagic compartment the major factor in determining exposure? Are the processes affecting uptake of POPs the same for animals living in the littoral and profundal zone?

We investigated the uptake of PCBs in signal crayfish (*Pacifastacus leniusculus*) and chironomid larvae (*Chironomus* sp.) as representatives for littoral and profundal benthic organisms in a trophic gradient of lakes. When studying between-lake differences, the variation between individuals could overshadow trends in the collected data. Therefore, an initial pilot study was made to investigate the intrapopulation variation within a crayfish population owing to differences in sex, size, and lipid content. However, we did not need to compensate for any of these variables, since none of them correlated with individual PCB concentrations in the population. By using both littoral and profundal animals, we wanted to investigate if processes affecting exposure, mechanisms of uptake, and concentrations of PCBs differed between the two compartments. Food source origin for benthic invertebrates may differ substantially between the littoral zone influence of terrestrial production and profundal areas where most energy input could be expected to originate from the pelagic photic zone.

Materials and methods

Study organisms

In this study, we used two different organisms, signal crayfish and chironomid larvae, as indicators of littoral and profundal food webs, respectively. The signal crayfish was introduced to Sweden in the 1960s and is today found in all types of freshwater ecosystems in southern Sweden and is common in both streams and lakes. It is generally found in the littoral zone but may inhabit hard bottoms in deeper areas of lakes. Diet examinations of crayfish have shown that individuals utilize a broad spectrum of food sources and shifts in diet may be induced by age and size, changing food resources, and changing environment (Nyström 1999). Chironomid larvae (Diptera: Chironomidae) are common in most lakes in southern Sweden and normally inhabite the sediment surface in the profundal zone. The larval stage may last for 1 to several years after which the insects metamorphose to the adult stage.

Intrapopulation variability in crayfish

During summer 2000, crayfish were collected from one population inhabiting a eutrophic pond in southern Sweden to examine if individual PCB levels were affected by intrapopulation variables such as sex, size, age, and fat content. Further, the variation of PCB concentration within the population was studied. From the crayfish population, a sample was drawn (n = 43) representing various sizes and both males (n = 24) and females (n = 19). The crayfish were collected using baited traps and were immediately frozen until analysis of lipid content and PCBs (see Sample preparation below).

Lakes

Lakes (n = 19) were investigated in the southern part of Sweden during August 2001. The lakes were chosen from different national lake databases to obtain high variation in

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Table 1. Descriptive limnological data of lakes included in the study.

Lake	Latitude (°N)	Longitude (°E)	tot-N ($mg \cdot L^{-1}$)	tot-P ($mg \cdot L^{-1}$)	pH	Secchi depth (m)	Chl *a* ($\mu g \cdot L^{-1}$)	Crayfish (*n*)	Chironomid sample
Båtsjön	58°9′	16°9′	1.55	93	9.4	0.6	85.0	6	×
Bysjön	58°11′	15°58′	0.95	58	7.3	0.9	41.1	6	×
Växjösjön	56°51′	14°48′	0.83	54	7.9	1.3	20.0	5	×
Råbelövssjön	57°21′	15°23′	0.62	53	8.0	1.6	19.3	0	×
Lilla Nätaren	57°46′	14°35′	1.16	45	8.8	1.3	16.5	6	×
Getryggen	58°11′	16°4′	1.14	44	9.2	0.8	42.8	6	×
Skärösjön	57°10′	14°51′	0.86	42	7.1	1.0	3.2	6	×
Bergsjön	55°5′	14°44′	0.79	31	6.4	0.8	20.7	5	×
Stora Nätaren	56°5′	14°14′	0.85	30	8.5	1.5	7.7	6	×
Tolgsjön	57°4′	14°48′	0.42	25	6.7	1.8	8.9	6	×
Sommen	57°47′	14°33′	0.44	21	8.3	4.9	15.2	6	×
Bunn	57°56′	14°30′	0.56	19	7.6	2.9	4.9	6	
Örsjön	57°56′	14°34′	0.54	17	6.4	2.0	8.7	6	×
Hövern	58°20′	16°5′	0.54	16	7.3	2.4	4.0	6	×
Helgasjön	57°0′	14°41′	0.53	15	6.8	2.2	11.5	6	
Ören	56°27′	13°57′	0.43	12	8.0	4.9	2.9	6	×
Horsfjärden	58°9′	15°54′	0.33	8	6.5	6.5	3.0	6	
Vitavatten	56°15′	14°35′	0.29	6	6.3	6.8	1.8	6	×
Vättern	58°45′	14°50′	0.39	6	7.8	6.0	1.3	6	
Skärlen	58°7′	14°59′	0.33	5	6.6	7.7	4.1	4	×

Note: All parameters of lake trophic status were highly correlated, positively for total nitrogen (tot-N), total phosphorus (tot-P), and chlorophyll *a* (Chl *a*), (r = 0.64 to 0.89) and negatively for Secchi depth (r = –0.51 to –0.74). The last two columns show number of crayfish included in samples (*n*) and whether samples of chironomids were collected (×).

trophic status indicated by total phosphorus (tot-P), total nitrogen (tot-N), and chlorophyll *a* (Chl *a*). Water chemistry data from the sample event during this study are provided in Table 1. Other criteria considered were maximum depth (>5 m) and lake area (>50 ha). Contacts were taken with landowners to establish a rough picture of the crayfish population number and distribution. In this study, only lakes with an established crayfish population were included. The populations were considered established if (*i*) mean catch per unit effort was above five individuals per trap and (*ii*) the population was older than 5 years.

In all lakes included in the study, the crayfish populations were monitored using Swedish Standards Institute recording catch per unit effort, individual crayfish size, gender, etc. Crayfish traps (n = 100) were used in lines of five traps with 10 m distance reaching 40 m out from the beach. Each trap attracts and catches adult signal crayfish in a circle within a radius of approximately 2 m (Abrahamsson and Goldman 1970). Hence, the total area monitored by the 20 lines was approximately 1300 m^2 in each lake. From each population (i.e., lake), a subsample of six crayfish (three individuals with body length 80–100 mm of each sex except in two lakes where only five and in one lake where only four individuals within proper size range where caught; see Table 1) was taken for analysis of PCB and lipid content, resulting in a total of 110 animals. The crayfish were individually frozen at –20 °C within 24 h after capture.

Chironomid larvae were collected from the deepest part of each lake. Sediments were pumped to the lake surface and sediments mixed with lake water were flushed out in a sieve (mesh size 0.5 mm) and the chironomid larvae were collected. Chironomids were collected to obtain one composite sample (of at least >1 g wet weight, one sample for every lake) for analysis of lipid content and PCBs. The samples were frozen and further treated similarly to crayfish samples.

Samples and measures of water chemistry (in the epilimnion) were taken at the same dates as the samples of benthic invertebrates and samples were determined according to Swedish standards (Swedish Standards Institute 1991). At the same time, Secchi depth was measured.

Sample preparation

Whole crayfish and pooled samples of chironomids were freeze-dried, homogenized, and kept dry (in closed containers at –20 °C) until time for extraction. The samples were Soxhlet extracted according to Bremle et al. (1995) using octachloronaphthalene as a surrogate standard. After extraction the solvent was reduced in a vacuum centrifuge. A subsample of the solvent was taken for lipid quantification and amounts were determined gravimetrically. The sample was redissolved in *n*-hexane and then transferred to an open column with two layers of silica gel for sample cleanup and separation of PCBs. The two layers had been treated with concentrated sulfuric acid and 1 mol $K_2CO_3 \cdot L^{-1}$, respectively. After column treatment, the solvent fraction containing PCBs was evaporated in a vacuum centrifuge, redissolved in isooctan, and stored in sealed capillary glass tubes containing copper grains (for elimination of sulfur). For every 12 samples extracted, a chemical blank was run. No PCBs were detected in the chemical blanks and thereby no blank correction was made.

PCB analyses

Samples were analyzed for PCBs by capillary gas chromatography – electron capture detection (Varian star 3400 cx electron capture detector, Varian, Inc., Palo Alto, Califor-

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nia) with a split–splitless injector, 25-m DB5 quartz capillary column (inside diameter 0.25 mm). PCB components were identified according to Schultz et al. (1989). The 18 predominant PCB congeners in the samples were included in ΣPCB in this study: International Union of Pure and Applied Chemistry (see Schultz et al. 1989) Nos. 52, 95, 101, 110, 149, 153, 138, 183, 128, 174, 177, 202, 180, 170, 201, 196, 194, and 206. Congeners were identified and quantified according to relative retention time and pentachlorbenzene was used as a standard for response factors for every run. External PCB standards of Clophen and Aroclor mixtures (Analytical Standards AB, Kungsbacka, Sweden) were included for every 10th sample for a quality check of both identification and quantification. Extraction efficiency for octachlornaphtalene was 94% ± 9% and no correction for recovery was made. The detection limits for ΣPCB were estimated to 1.1 ng·g dry weight^{-1} (sample size 1 g).

Statistical analysis

All concentration data on PCBs in crayfish or chironomids were log transformed owing to skewed distributions (Newton 1988) before statistical analysis. Possible relationships between variables were carried out by linear regression when the x variable could be expected to influence the y variable but not vice versa; otherwise, Pearson correlation was used. The crayfish intrapopulation variables were further tested using the data from lakes in an ANCOVA approach where log PCB concentration (dry weight) was the dependent variable in the analysis, lake was the independent grouping variable, and lipid content was the covariate. Comparisons of PCB concentrations between sexes were made using t tests in the intrapopulation study and paired t tests when comparing lake data.

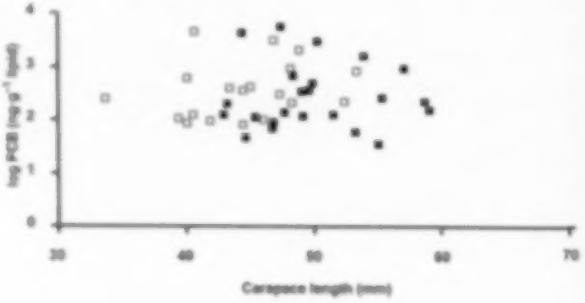
The congener profile is presented as mean values normalized to the concentration of PCB 153 where mean PCB 153 concentration was set to 1. Mean values of individual congener concentrations were calculated on all samples of crayfish (n = 109) and chironomids (n = 15). The reason for normalizing for PCB 153 was that this congener had the most stable high concentration of the congeners present in both species. Normalization relative to PCB 153 has been used in earlier work (e.g., Derocher et al. 2003).

Results

Intrapopulation variability in crayfish

PCB concentrations in crayfish from the pond population (n = 43) varied between 3 and 198 ng·g dry weight^{-1}. The median concentration in the population was 12.5 ng·g dry weight^{-1}. As lipid content varied between 1% and 18% of the dry weight, individual PCB concentrations varied from 34 to 10 600 ng·g^{-1} on a lipid basis. Median concentration was 247 ng·g lipid weight^{-1}. The PCB concentration did not differ between male and female crayfish in the population (t test: df = 1, t = 0.133, p = 0.35), nor did lipid content (t test: df = 1, t = 4.0, p = 0.27). No correlation was found between size and lipid content (Pearson correlation: df = 42, r = 0.26, p = 0.09) of the crayfish or the concentration of PCB (Fig. 1) (Pearson correlation: df = 42, r = 0.25, p = 0.11). Lipid content was not correlated with carapace length (size of crayfish) (Pearson correlation: df = 42, r = –0.05, p = 0.78).

Fig. 1. Scattergram showing concentrations of PCBs (ΣPCB) in signal crayfish (*Pacifastacus leniusculus*) of increasing size in the single population data. Males are represented by solid squares and females by open squares. The linear regression shows no relationship between crayfish size and ΣPCB (r^2 = 0.15, p = 0.32, n = 43). This was also the case when data were separated into males (r^2 = 0.05, p = 0.29, n = 24) and females (r^2 = 0.06, p = 0.29, n = 19).



We tested the general effect of lipid content on ΣPCB concentration in crayfish from all of the lakes in an ANCOVA. Log PCB concentration (dry weight) was the dependent variable in the analysis, lake was the independent grouping variable, and lipid content was the covariate. Since the interaction between lake and lipid was not significant ($F_{11,71}$ = 0.99, p > 0.47), this was omitted from the analyses. The ΣPCB concentration differed significantly between lakes (p < 0.001), but no significant effect of lipid content could be found on ΣPCB concentration ($F_{1,89}$ = 1.99, p > 0.16). The lipid content in lake crayfish varied between 0.5% and 13% (dry weight).

No difference could be found between crayfish males and females within lake data in ΣPCB (paired t test: df = 18, t = 0.94, p = 0.36), lipid content (paired t test: df = 18, t = 1.78, p = 0.09), and lipid-based ΣPCB (paired t test: df = 18, t = 0.16, p = 0.87).

Lake trophy related variability

The tot-P in the lakes varied from 5 to 93 µg·L^{-1}, tot-N from 0.3 to 1.6 mg·L^{-1}, and Chl a from 1.3 to 85 µg·L^{-1}. The Secchi depth varied from 0.6 to 7.7 m. All parameters of lake trophic status were highly correlated, positively for tot-N, tot-P, and Chl a (Pearson correlation: df = 18, r = 0.64–0.89, p < 0.01) and negatively for Secchi depth (Pearson correlation: r = –0.51–0.74, p < 0.01) (Table 1).

PCB concentrations varied between 1.5 and 260 ng·g dry weight^{-1} in crayfish (n = 110) in the studied lakes with a median of 8.4 ng·g dry weight^{-1} and between 4.0 and 780 ng·g dry weight^{-1} in chironomid larvae (n = 15) with a median of 14 ng·g dry weight^{-1}. The ΣPCB concentrations in chironomid larvae were negatively related to lake trophic status (tot-P, linear regression: df = 14, r^2 = 0.30, p = 0.03) and significance increased when values were lipid normalized (Fig. 2*b*) (linear regression: df = 14, r^2 = 0.38, p < 0.01). The lipid content in chironomid larvae partly explained PCB concentrations (linear regression: df = 14, r^2 = 0.41, p < 0.01). Lipid content in chironomids did not corre-

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Fig. 2. (*a*) Mean concentration of PCBs (ΣPCB) in signal crayfish (*Pacifastacus leniusculus*) from lakes of increasing trophic status. Females ($n = 3$) and males ($n = 3$) were analyzed from each lake. The analysis is based on mean values, and error bars represent ±1 SD (linear regression: $r^2 = 0.08$, $p = 0.29$, $n = 19$). (*b*) ΣPCB in chironomid larvae from lakes of increasing trophic status (linear regression: $b = -0.65$, $r^2 = 0.42$, $p = 0.001$, $n = 15$).

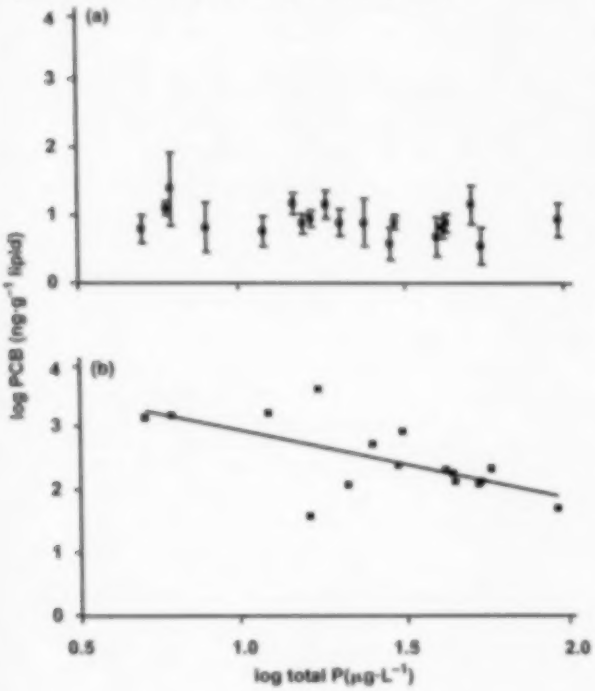
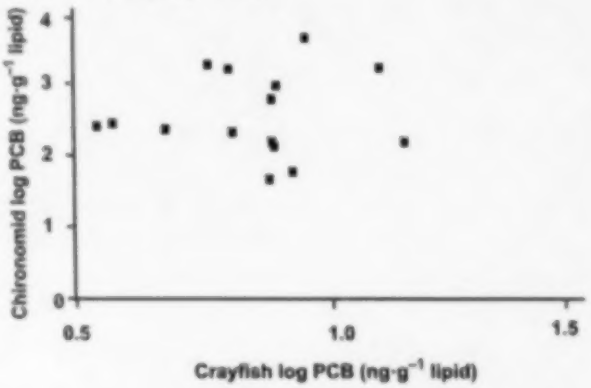


Fig. 3. Scattergram showing mean concentration of PCBs (ΣPCB) for signal crayfish (*Pacifastacus leniusculus*) versus ΣPCB in pooled chironomid samples in lakes ($n = 15$). No correlation could be found between the two compartments (Pearson correlation $r = 0.18$, $p = 0.52$).



late with lake trophy in this study (Pearson correlation: df = 14, $r = 0.07$, $p = 0.80$). Lipid content in chironomid larvae samples ranged between 7% and 21% dry weight.

There was no relationship between lake trophic status (tot-P) and mean ΣPCB concentrations in crayfish on a dry weight basis (linear regression: df = 18, $r^2 = 0.08$, $p = 0.29$) or when values were lipid normalized (Fig. 2*a*) (linear regression: df = 18, $r^2 = 0.03$, $p = 0.56$). The lipid-based ΣPCB concentrations in crayfish and chironomid larvae within lakes were not correlated (Fig. 3) (Pearson correlation: df = 14, $r = 0.09$, $p = 0.76$). The PCB concentrations in chironomids were higher than in crayfish within lakes (paired *t* test: df = 14, $t = -10.8$, $p < 0.001$).

The PCB congener distribution showed slight differences in crayfish and chironomid samples (Fig. 4). The three dominating congeners in crayfish were the medium-chlorinated congeners PCB 149, PCB 153, and PCB 138. Dominating congeners in chironomids were the medium-chlorinated PCB 153 and the two highly chlorinated congeners PCB 180 and PCB 196.

Discussion

Lake trophy

Contrary to what could be expected, given the results from earlier experimental studies (Gilek et al. 1996; Björk and Gilek 1997; Gunnarsson et al. 2000), we found that PCB concentrations in profundal benthos (chironomid larvae) were negatively related to lake trophic status. In earlier experiments, marine filter-feeding mussels were exposed to additions of algae at different concentrations. The concentrations of PCBs in mussels increased with increasing algae biomass, indicating a positive relationship between trophic status of the water and bioaccumulation of PCBs in benthic animals. Investigations of the relationship between trophic status of waters and POP accumulation in benthic animals have so far been restricted to a few experimental studies (summarized in Gunnarsson et al. 2000). One of the conclusions from these studies is a concern that increasing eutrophication may increase POP loads in benthic organisms because increasing settling of organic carbon rich particles increases the bioturbation of sediments. We found that different compartments of the benthic food web may differ considerably in bioaccumulation of PCBs within lakes. While the PCB concentrations of profundal organisms were negatively correlated with lake trophy, the PCB concentrations in littoral crayfish did not show any relationship with changing nutrient regimes. The lack of correlation within lakes between the two compartments indicates that different processes are governing the uptake of PCBs in littoral and profundal organisms.

A negative relationship between lake trophic status and ΣPCB concentrations in pelagic biota has been reported for freshwater phytoplankton (Berglund et al. 2001*a*, 2001*b*), zooplankton (Taylor et al. 1991), and fish (Larsson et al. 1992). The main explanation for decreasing levels of POPs in the piscivorious northern pike (*Esox lucius*) of eutrophic systems was increasing individual growth rates in the pike population (Larsson et al. 1992). Studies on pelagic plankton led to a hypothesis that a high growth rate of phytoplankton in nutrient-rich waters affects the concentration of POPs, i.e., that cell division rates of phytoplankton exceed the uptake kinetics of POPs (e.g., see Larsson et al. 2000) This restriction in uptake efficiency may lead to lower concentrations of POPs in the first link of the food chain in eutrophic environments (Larsson et al. 2000). However, Berglund et al. (2001*b*) reported that differences in phyto-

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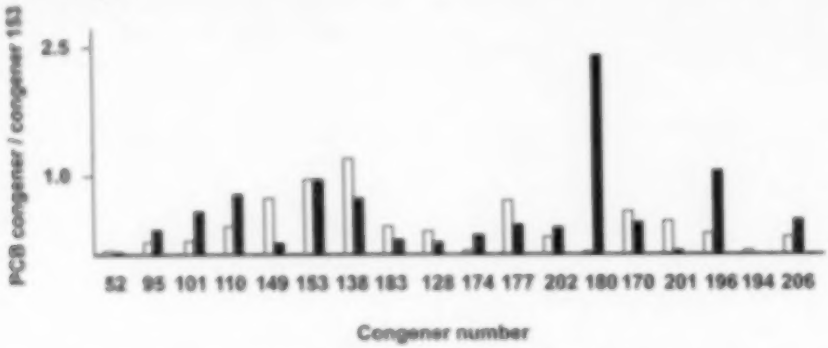
Fig. 4. Congener pattern of the 18 most common PCBs in signal crayfish (*Pacifastacus leniusculus*; $n = 110$) (open bars) and chironomid larvae ($n = 15$) (solid bars). Mean values are calculated as individual congener concentration (ng·g lipid^{-1}) divided by congener 153 concentrations for each sample.



plankton lipids might explain most of the variance in ΣPCB concentrations. The higher levels of POPs in the phytoplankton of oligotrophic systems could thereby be explained by differences in species composition and lipid content as a response to nutrient stress. So far, investigations made on the relationship between bioaccumulation of POPs in biota and lake trophy have been focused on pelagic species.

After being incorporated in pelagic biota and (or) organic matter, parts of the particle-bound POPs will be transported to the bottom of lakes by sedimentation (see Fig. 5). The concentration of POPs in settling particles (i.e., sedimentating seston, see above) has been reported to be dependent on lake trophic status with higher concentrations in oligotrophic lakes. In Larsson et al. (1998), a comparison of a eutrophic and an oligotrophic lake showed that microbial breakdown of the organic matter concentrates POPs in the remaining organic matrix. The efficiency of this magnification process was calculated to be about four times more effective in the oligotrophic lake compared with the eutrophic lake. Hence, particles reaching the sediment have higher concentrations of POPs in oligotrophic systems, but owing to higher sedimentation rates in eutrophic lakes, the total amount reaching sediments is higher (Berglund et al. 2001*a*).

Internal lake processes redistribute PCBs between water, sediment, and biota (see below). There appears to be an intense (re-)cycling of organic carbon and PCBs at the sediment–water interface and the layer above, the nepheloid layer (Baker and Eisenrich 1985). The recycling of organic carbon and POPs has also been reported to be dependent on the trophic status of lakes; more organic carbon in the sediment will give a higher biological activity and thereby more bioturbation in eutrophic systems (e.g., Gunnarsson et al. 2000). However, bioaccumulation of sediment-derived POPs in chironomids and tubificides has been shown to be inversely related to organic carbon content in sediments (Bremle and Ewald 1995). Owing to their lipophilicity, POPs have high affinity for organic-rich material and thereby a low probability of being bioaccumulated in chironomids and tubificides in organic carbon rich sediments. Our data could in the light of these two findings give some support to the conclusion that high organic carbon content in sediments binds the PCBs and makes them less available for bioaccumulation in sediments with high organic carbon content (i.e., eutrophic lakes).

Problems with finding a reliable equilibrium between benthic biota and POPs in sediments have been reported from several studies (e.g., Bremle and Ewald 1995; Gunnarsson et al. 1999). Further, when Bremle and Ewald (1995) compared the PCB congener patterns in chironomid samples from different parts of a lake, the variation could not be explained by congener variation in the sediments from the same locations alone. Instead, the variation was explained by varying quality of organic carbon, which influenced PCB sorption, and thereby bioaccumulation. Higher levels of POPs in benthic biota than expected from equilibrium calculations with sediments have also been explained with selective feeding on organic-rich and (or) highly contaminated particles (Gunnarsson et al. 1996, 1999; Morrison et al. 1996). In surface sediments, where most benthic invertebrates feed, particles with the highest nutritional value are newly settled particles (Larsson et al. 1998). After settling on the sediment surface, particles undergo rapid microbial transformations or breakdown. This transformation of particles rapidly decreases both organic carbon content and POP concentration in the surface sediment. Baker et al. (1991) showed that settling particles have 10–100 times higher levels of POPs compared with resuspended sediments. Thus, higher concentrations of PCBs in benthic invertebrates than to be expected from equilibrium calculations with sediment could be explained by selective feeding on fresh untransformed material from the pelagic compartment.

We suggest that the found negative relationship between PCB concentration and lake trophic status in the profundal organism is simply a mirror of the relationship found for pelagic biota. High concentrations of PCBs in the pelagic food webs, and especially in phytoplankton, in lakes will result in high concentrations in profundal benthic organisms regardless of varying organic carbon content in the sediment. The profundal organism used in this study, chironomid larvae, feeds in the upper layers of the sediment (Jonasson 1972) and is thereby directly exposed to settling material from the pelagic environment. Consequently, independent of organic carbon content or other biochemical variables in the sediment, PCB concentration and congener distribution in

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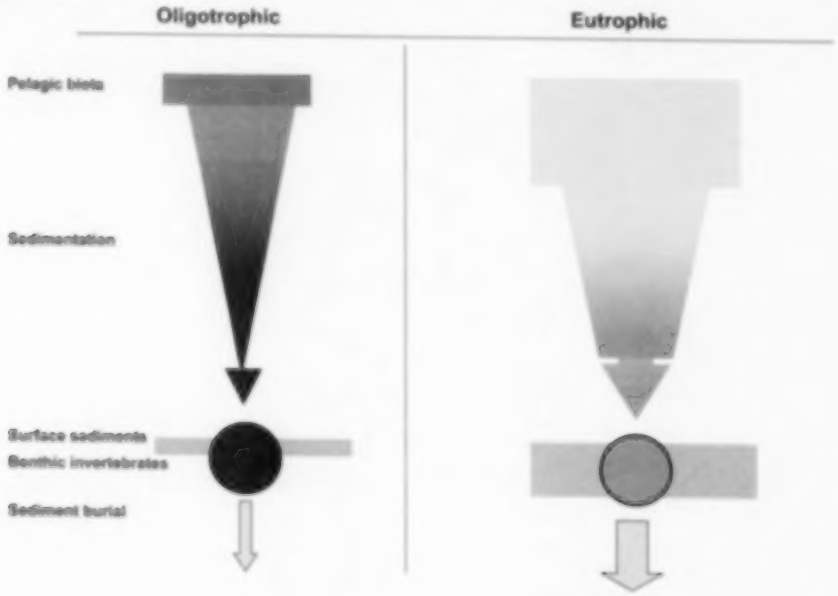
Fig. 5. Conceptual view of fate of PCBs and internal pelagic–profundal processes in oligotrophic and eutrophic lakes. The flow of organic matter is represented by the size of boxes and arrows and the PCB concentration by the intensity of the grayscale. In the pelagic compartment of the eutrophic lake, there is a high amount of organic matter (biomass) but low PCB concentrations (e.g., Taylor et al. 1991). During sedimentation, degradation of organic matter magnifies PCB concentrations (Baker and Eisenrich 1985; Larsson et al. 1998) and this process is more efficient in the oligotrophic lake (Larsson et al. 1998), leading to higher PCB concentrations in freshly settled material. PCB concentrations in surface sediments are unrelated to lake trophy but amounts are positively related to lake trophy owing to the higher amount of settling of organic matter in eutrophic systems (Berglund et al. 2001*a*). PCBs can be buried into deep sediments and inactivated together with organic carbon (eutrophic lake: Jeremiason et al. 1999; Berglund et al. 2001*a*) or recycled back to the ecosystem owing to partitioning and bioturbation (oligotrophic lake: Gunnarsson et al. 2000). The results from this study show that the PCB concentration in benthic invertebrates feeding on the surface sediment is higher in the oligotrophic system, represented by the circle in the sediment box.



profundal sediment surface feeding biota will be determined by processes in the pelagic compartment and during sedimentation.

Profundal and littoral benthic food webs

Although we compared two different organisms, one in the littoral zone and one in the profundal zone, slight differences in congener pattern and the absence of a correlation between PCBs in chironomids and PCBs in crayfish indicate that different processes determine PCB accumulation in the two compartments. Owing to the hydrophobic nature of PCBs, they associate with particles and sorption is mainly governed by hydrophobicity of the compound and lipid and (or) organic content of the particle (Swackhamer and Skoglund 1993; Berglund et al. 2001*a*). During sedimentation, microorganisms process particles and less lipophilic congeners can be recycled back to the pelagic environment (Baker et al. 1991). The process leads to a higher proportion of highly lipophilic substances in particles entering the sediment surface (Baker et al. 1991). In Bremle and Ewald (1995), congener profiles in chironomid samples similar to those found in this study are reported. Proportionally high concentrations of highly chlorinated congeners compared with sediments were found. The differences in congener distribution could be a result of that profundal benthos mainly feeds on settled pelagic phytoplankton. In littoral food webs, the major source of energy is primary production in macrophytes and periphytic algae with the addition of terrestrial production (Wetzel 1983). Both macrophytes and periphyton are important food sources for signal crayfish (Nyström 1999). Differences in species composition and thereby lipid quality and quantity in macrophytes and periphyton could change between lakes of different trophic status and species composition as found in phytoplankton. However, accumulation of PCBs in macrophytes and periphyton is a poorly investigated area. Vanier et al. (1999) reported PCB accumulation in macrophyte roots to be directly dependent on PCB concentration in the sediment, while the uptake in shoots is more likely dependent on other variables such as concentration in the surrounding water. Further, uptake in roots was proposed to be important in transporting sediment-buried PCBs back to biota in lake ecosystems. It can only be speculated that accumulation of PCBs in macrophytes and periphyton is independent of lake trophy and could thereby explain the lack of correlation between (*i*) crayfish uptake of PCBs and lake trophy and (*ii*) PCB accumulation in crayfish and that in chironomids within lakes.

Alternatively, the differences between the two compartments can be explained by terrestrial input of energy and PCB to the ecosystem. Especially nutrient-poor lake ecosys-

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tems have low production of autotrophic energy and may drive the system to be more dependent on terrestrial energy input (Wetzel 1983). The effect of terrestrial input of energy and PCBs is probably most obvious in the littoral food chain and could contribute to the differences between the two compartments. Changes to a more terrestrial-based diet especially in littoral organisms in oligotrophic lakes as well as changes in food web structure with changing lake trophy (Mosmot 1995; Nyström 1999) could thereby change the exposure of PCBs to crayfish.

Benthic–pelagic coupling

Berglund et al. (2001*b*) reported that the negative correlation between lipid content in primary producers and ΣPCB with lake trophy was not transferred to higher trophic levels, zooplankton and juvenile zooplanktivorous fish, in the pelagic food chain. This finding indicates that the decreasing concentrations of PCB with increasing lake trophy found in higher trophic levels, e.g., piscivorous fish (Larsson et al. 1992), are not due to a pelagic food chain mediated effect of bioaccumulation in phytoplankton. Instead, this relationship can, which has indeed been proposed by several authors (e.g., Larsson et al. 1992, 2000; Skei et al. 2000), be explained by excessive nutrient loads that increase individual growth rates and that high growth rate leads to a second level of growth dilution. These two processes could maybe work separately but with the same result giving decreasing levels of PCBs in the organisms with increasing eutrophication in the organisms. Alternatively, or complementary to, benthic invertebrates, such as chironomid larvae, act as transport vectors of the phytoplankton effect to higher trophic levels in the pelagic food web. As suggested earlier in this paper, pelagic processes could explain the negative relationship between levels of PCB in chironomid larvae and lake trophy. Consequently, consumption of chironomids by fish could act as a feedback loop of settled PCBs and complement the expected transport route phytoplankton–zooplankton–fish in the pelagic food chain. A feedback loop of PCB by phytoplankton – chironomids – benthivorous fish – pike could be an alternative or complementary explanation to the "growth dilution" hypotheses presented in Larsson et al. (1992). A possible transport of PCBs from sediments to fish via benthic invertebrates has been reported in other studies (e.g., Bremle and Ewald 1995; Gunnarsson et al. 2000).

Intrapopulation variability

In the part of the study where the variance in PCB concentration within one crayfish population was studied, we could not find any correlation with individual-based variables. The age of crayfish is hard to determine because growth varies considerably with food quality and quantity, water temperature, and individual size (Belchier et al. 1998). The lack of correlation between size (age) and PCB concentration in the crayfish population, which has been shown in freshwater fish (Boileau et al. 1979; Larsson et al. 1991; Madenjian et al. 1994), can be explained by the fact that, contrary to fish, the crayfish has continuously moulting stages during its life span. The process is energy demanding and, probably, means a total utilization of any energy stores, like those containing lipids. Lipophilic pollutants like PCBs may then be fully or partly eliminated with cycles of PCB accumulation occurring from moult to moult, not over the whole life span as, e.g., in fish. Hence, no effect of age and size can be found in lipid content and (or) accumulation of PCBs. In fact, the different life history, compared with, e.g., fish, can explain the lack of differences between males and females as well. If lipids are not continuously stored during life, no differences can be established between sexes that are commonly found in other organisms owing to the loss of lipids during egg production and depuration (Harding 1986; Larsson et al. 1992; Johnston et al. 2002). This suggests that the positive relationship between fat content and accumulation of POPs in biota can be an effect of life history and a continuous storage of lipids during life that will result in increased accumulation of POPs with time. This process is not valid for crayfish and probably not for any aquatic invertebrate with continuously moulting stages.

In conclusion, bioaccumulation of PCBs in crayfish was unrelated to size, sex, and lipid content. We propose that internal lake processes in the pelagic environment directly influence PCB concentration of profundal chironomids. The negative relationship between lake trophy and pelagic species was also found in sediment surface living chironomids in the profundal zone. PCB concentrations in crayfish living in the littoral zone seemed unaffected by lake trophy and the concentrations were not correlated with chironomid concentration within lakes. Therefore, we speculate that different factors are involved in the exposure of PCBs in the two compartments.

Acknowledgements

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The schooling and foraging ecology of lake herring (*Coregonus artedi*) in Lake Opeongo, Ontario, Canada

S.W. Milne, B.J. Shuter, and W.G. Sprules

Abstract: We used a combination of suspended gill nets and hydroacoustics to investigate the schooling behaviour of lake herring (*Coregonus artedi*) in Lake Opeongo, Ontario, Canada. Lake herring form schools during the day but are dispersed at night and this change occurs at a light threshold of roughly 0.04 lx. Schools range in maximum linear dimension from 100 to 2300 cm with the majority under 1000 cm. The light threshold for school formation is well below that at which their principal predator, lake trout (*Salvelinus namaycush*), are able to detect prey. This suggests that schooling may provide advantages in addition to predator avoidance. We observed that lake herring stomachs were fuller during the day than at night, indicating that schooling herring forage more efficiently during the day than individual herring do at night. Furthermore, herring stomach fullness increased with school size, suggesting that schooling enhances foraging opportunities for individual members. We speculate that this is due either to social facilitation of feeding when herring are in the presence of conspecifics, or to corporate vigilance, or "many eyes", which allows individual fish to spend less time being alert to predators and more time feeding.

Résumé : Nous avons utilisé une combinaison de filets maillants suspendus et de techniques hydroacoustiques pour étudier le comportement de formation de bancs chez le cisco de lac (*Coregonus artedi*) au lac Opeongo, Ontario, Canada. Les ciscos forment des bancs durant la journée et se dispersent durant la nuit; le changement se produit à un seuil de lumière d'approximativement 0,04 lx. Les bancs varient en taille linéaire maximale de 100 cm à 2300 cm, la plupart atteignant moins de 1000 cm. Le seuil lumineux pour la formation des bancs est bien inférieur à celui auquel leur prédateur principal, le touladi (*Salvelinus namaycush*), est capable de détecter ses proies. Cela laisse croire que la formation de bancs peut procurer des avantages autres que l'évitement des prédateurs. Nous avons observé que les estomacs de ciscos de lacs sont plus remplis durant le jour que la nuit, ce qui indique que les ciscos en bancs s'alimentent plus efficacement le jour que les ciscos solitaires la nuit. De plus, les estomacs sont d'autant plus remplis que les bancs sont de grande taille, ce qui indique que la formation de bancs multiplie les occasions de s'alimenter pour les membres du banc. Nous pensons que cela est dû ou bien à une facilitation sociale de l'alimentation lorsque les ciscos sont en présence de poissons de même espèce, ou alors à la vigilance collective par des « yeux multiples » qui permet à chaque poisson de passer moins de temps en alerte vis à vis de ses prédateurs et plus de temps à s'alimenter.

[Traduit par la Rédaction]

Introduction

Traditional models of fish production incorporate system-wide averages of predator and prey abundances and assume that spatial arrangements of organisms are homogeneous within a constant environment (Brandt et al. 1992). They also assume that foraging is a stochastic process, with predators randomly encountering prey that are randomly distributed in the water. In fact, prey fish distributions are often patchy in space and time, and in particular, schooling is so prevalent in fish that there must be clear adaptive advantages to such spatial behaviour (Biette and Geen 1980; Huth and Wissel 1992). Fish aggregated in schools experience lower rates of encounter with predators and are less likely to be consumed if attacked because predators quickly become satiated and remaining prey can escape (Pitcher 1986). "Many eyes" within a school increase the chance of detecting predators (Turner and Pitcher 1986) as well as locating food (Pitcher 1986; Peuhkuri et al. 1995). On the other hand, there are costs to schooling, such as increased visibility to

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predators (Pitcher 1986; Litvak 1993) and increased intraspecific competition.

The lake herring (*Coregonus artedi*; hereinafter referred to as herring) is a schooling planktivore common in colder lakes throughout Canada and the northern United States (Scott and Crossman 1973). It was introduced into Lake Opeongo, Ontario, in 1948 to improve the quality of sport fishing for lake trout (*Salvelinus namaycush*) (Matuszek et al. 1990) and quickly established as the primary prey species for lake trout. Herring continue to act as an important link between lake trout and the zooplankton community within the system (Matuszek et al. 1990).

The purpose of our investigation was to identify the mechanisms responsible for the schooling behaviour of herring in Lake Opeongo. Do they school solely as a function of predator avoidance or are there other benefits to the behaviour? In particular, we will test the hypotheses that (*i*) schooling increases with light intensity in the water column, (*ii*) schools disperse when light levels are too low for lake trout to detect herring, (*iii*) herring feed more at night, when the threat of predation is minimized, and (*iv*) food consumption increases with school size.

Methods

Study lake

Lake Opeongo is the largest lake in Algonquin Provincial Park, Ontario, with an area of approximately 5500 ha and over 115 km of shoreline. It is an oligotrophic lake with a maximum depth of 53 m and a mean depth of 14.8 m. The lake comprises three major basins that are similar in area and joined by small channels. The fish community in the lake is quite diverse, but our study focuses on the lake herring and its principal predator, the lake trout. Our work was concentrated within a 800 m × 800 m site in the northern section of the south basin, where water depth was approximately 20 m.

Fish sampling

One of the principal objectives of our study was to obtain information on the size and spatial distribution of herring schools in the wild. Such observations are difficult to make because the size and spatial position of fish schools can change on a continuous basis and over relatively large spatial scales. One option is the use of suspended gill nets that provide a "snapshot" of the spatial pattern of fish at the time of capture as well as a sample of fish for species identification and relevant individual measurements. On the other hand, such invasive techniques could affect apparent school size and shape, and gillnet dimensions would have to match the typical size and spatial patterning of schools for accurate assessments to be made. Hydroacoustic techniques provide better spatial coverage, but calibration of the signal to the size and species of fish encountered is challenging, and determination of school dimensions depends on the nature of edge-detection algorithms used in analysis of the acoustic data. In this study we chose to use simultaneous gillnetting and hydroacoustics to acquire information on herring schools, and to seek concordance in the results from these approaches for making the most rigorous estimates of school metrics.

Gillnetting

Gillnetting was done during 1999 in spring (10–23 May), when thermal stratification was weak, in summer (1–17 July), when thermal stratification was strong, and in fall (8–18 October), immediately before overturn. Monofilament gill nets 45 m long and 2.2 m high and of 25-mm stretched mesh were used to capture herring. Nets were deployed at chosen depths by using a combination of float and anchor lines. The site was sampled twice during each sampling day — in midafternoon (from 1201 to 1745) and at night (from 2300 to 0422 of the same or following day). These sampling periods were chosen to obtain the greatest contrast in schooling behaviour and to avoid the crepuscular period of transition. During each sampling period, nets were set at three sampling depths: 4 and 16 m plus the depth of the 12 °C isotherm, the preferred temperature for lake herring (Rudstam and Magnuson 1985). The depth of the 12 °C isotherm ranged from 1 to 11 m through the study period. Nets were set 150 m apart parallel to one another and perpendicular to the maximum fetch in the basin. Nets were set for short periods — a mean of 34 min during the day and 21 min during the night — to minimize deterioration of herring stomach contents and minimize the number of schools caught at any one time. Over the study period, a total of 120 nets were set (6–8 per depth × 3 depths × 2 periods (day and night) × 3 seasons).

Immediately after the nets were retrieved, the individual fish were removed and their position in the net was marked with a unique identification number. Stomachs were removed and preserved in 10% formalin. The body was kept for later sex determination and measurement of fork length, total length, and mass without the stomach.

Hydroacoustic analysis of herring spatial patterns

A hydroacoustic survey of the northern section of the South Arm of Lake Opeongo was completed during the day and night in May, July, and October. Survey transects were designed to overlap the suspended gill nets both spatially and temporally. A split-beam Simrad EY500 120-kHz hydroacoustic system with an ES120-7° transducer was used to record the spatial distribution and behavioural changes of individual herring as well as herring schools. All acoustic data were analyzed using EchoView® version 1.51.20 (Sonardata Tasmania Pty Ltd. 1999*a*) and schools were detected and measured using the School Detection Module within EchoView® (Sonardata Tasmania Pty Ltd. 1999*b*). Schools were detected by the downward-looking acoustic transducer as the survey vessel proceeded along a sampling track. The School Detection Module defines a school by including only pixels that are (*i*) contiguous and (*ii*) have an echo strength that exceeds a minimum (we used –55 dB). The software computes the height of a school at the random point of encounter by subtracting the depth of the shallowest pixel in the defined region from the depth of the deepest one. The length of the school is computed by using the Pythagorean theorem to subtract the global positioning system (GPS) coordinates of the first pixel encountered in the defined region from the last one encountered. EchoView® can correct for errors in these dimensions caused by school depth and position relative to the acoustic beam, but we did not do this because Lake Opeongo is shallow enough that

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beam angles are narrow and pulse lengths are short and errors are consequently small.

There are two common fish species in Lake Opeongo that form schools — lake herring and yellow perch (*Perca flavescens*). However, yellow perch are not known to occupy the cool-water pelagic regions that we sampled in this study, and none was captured in the gill nets. We thus assumed that any acoustically detected schools were of herring. Only those single targets with strengths between –47 and –37 dB were included in the nighttime analyses because Love's (1977) general equation predicts that fish in the size range of Lake Opeongo herring (minimum, mean, and maximum total length = 99, 144.5, and 175 mm, respectively) have target strengths in this range.

Spatial analysis of herring captured in gill nets

All captured fish were wedged in the meshes of the gill net and hence the direction of travel prior to capture could be ascertained. Most fish aggregations were composed of fish travelling in a uniform direction, but in some instances aggregations included individuals oriented in both directions. In all such cases the majority of fish were oriented in one direction and the few fish directed the opposite way strongly overlapped the main aggregation. We interpreted these aggregations to represent single schools of fish that encountered the net from one direction but with a few stray individuals reversing direction, perhaps in the confusion of the encounter with the gill net. We thus combined fish travelling in both directions in the calculation of an index of aggregation (IA). We used nearest neighbour (NN) analysis (Clark and Evans 1954) to assess the spatial aggregation of herring captured in the gill nets. The IA was computed as R_A/R_E, where R_A is the observed median NN distance and R_E is the median NN distance expected for a random set of locations within the net. A random set of point locations within an unbounded two-dimensional area has an expected IA of 1.0, a uniform set has an expected IA greater than 1.0 (maximum 2.16), and a clumped set has an expected IA less than 1.0 (minimum approaches 0). We constructed the following procedure to identify observed IAs that differed statistically from that expected for a random set of fish locations. First, we determined the distribution of R_E, the expected distance for random observations, for each possible sample size (total number of fish captured in a net) by randomly and independently placing a number of points equal to the sample size in a simulated 4500 cm × 220 cm rectangle (the dimensions of gill nets), computing the median NN distance and repeating this procedure 10 000 times. Then, for each observed NN value we estimated the probability that it came from a random spatial distribution as the proportion of R_E values in the simulated distribution (for the appropriate sample size) that exceeded the observed NN value. This probability was then assigned to the IA value calculated from the observed NN value. Observed values based on fewer than six fish were not included in this analysis because we found the simulated R_E distributions to be unstable for samples sizes less than six, even after 10 000 iterations. We did not need to make additional corrections for edge effects in these analyses (Boots and Getis 1988) because our numerically derived estimates of R_E already included the edge effects associated with a bounded area equal in size to that of our gill nets.

Given the wide variety of spatial patterns of herring in the gill nets, we decided to calculate the maximum linear dimensions of captured herring schools using the following algorithm. For each gill net we computed the median Euclidean distance between each fish and all others in the net. We then removed from the analysis those fish for which the median distance was in the upper 10% of the set of distances (to avoid situations such as a single fish distant from an aggregation inflating school size). The maximum median distance for the remaining fish was then computed as the length of the school in the net. This calculation will overestimate school size if there is more than one clump of fish in a net and will underestimate school size if there is a single, well-prescribed clump of fish (because outliers are removed).

Lake trout tracking

Eight adult lake trout were implanted with ultrasonic tags (CTT-83-2, Sonotronics, Tuscon, Arizona, USA) and released back into the South Arm of Lake Opeongo during the spring of 2000. During August 2000, each tagged trout was followed over a 12- to 20-h period, with geographic position and time recorded every 10–12 min. Light intensity was continuously measured at the surface using HOBO® HLI light loggers (Onset Computer Corporation, Bourne, Massachusetts, USA). Movement ($m \cdot min^{-1}$) of lake trout was determined by measuring the Euclidean distance and time elapsed between sequential coordinate locations. Observations were classified into nighttime (surface light intensity <0.04 lx) and daytime (>320 lx), the mean speed was computed for each day and night observation period, and a Kruskal–Wallis test was used to test the hypothesis that mean speed was the same for daytime and nighttime. All lake trout tracking data were provided from unpublished data by L. Flavelle (Department of Biology, University of Waterloo, Waterloo, ON N2L 3G1) and T. Janoscik (Department of Biology, University of Toronto at Mississauga, Mississauga, ON L5L 1C6).

Physical and zooplankton sampling

A light meter (Hobo® HLI) was used to continuously measure surface light intensity at a stationary point in the sampling site every minute during the sampling period. Three additional light meters were submerged at approximately the same depths as the gill nets. This information, in addition to estimates of the light-absorption coefficient taken from vertical profiles with a light meter (LI-192SB quantum sensor, LI-COR Inc., Lincoln, Neb., USA) every 2 weeks, was used to estimate the light intensity at depth over the time the nets were set. Temperature and dissolved-oxygen profiles were measured at 1-m intervals at the site (Model 58 oxygen/temperature meter, Yellow Springs Instruments Inc., Yellow Springs, Ohio, USA). These temperature data were used to establish the depth of the 12 °C isotherm.

Zooplankton samples were pumped from the water column at each of the three netting depths during both daytime and nighttime sets. Forty litres of water were pumped through a 110 µm mesh sieve, the sieve was rinsed into a jar, and the sample was preserved in a 2%–4% sugar-buffered formalin solution.

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Processing of fish stomachs and zooplankton

We randomly selected a minimum of 10 herring stomachs (or all stomachs if fewer fish were captured) from each of the gillnet samples used in the aggregation analysis. The contents of each stomach were placed in a 53 µm mesh filter, rinsed to remove residual preservative, and added to a "plankton shaker" (after Alden et al. 1982) for gentle filtering through four sequential Nitex sieves of 500, 400, 202, and 53 µm mesh. After the shaking was completed, the filters were removed and the contents rinsed into preweighed aluminium drying pans. After filtering, the contents of the 53 and 202 µm mesh filters were rinsed into separate drying pans and the contents of the 500 and 400 µm mesh filters were pooled into a third pan. Samples were dried at 60 °C for 20–28 h, removed, and weighed on a Sartorius 1207 MPZ digital balance. Total dry mass of the herring stomach contents was calculated by summing the masses of individual fractions.

Entire zooplankton samples pumped from the water column were rinsed through a 53 µm mesh sieve, dried, and weighed as above.

Statistical analysis of prey consumed

There was no evidence of a relationship between fish size and mass of stomach contents (separate analyses of covariance (ANCOVA) of stomach contents among gill nets with fish length as the covariate for each of the six season / time of day combinations), probably because the size range of herring in Lake Opeongo is quite narrow (111–150 mm for fish used in this ANCOVA). Hence, we ignored fish size in all subsequent analyses.

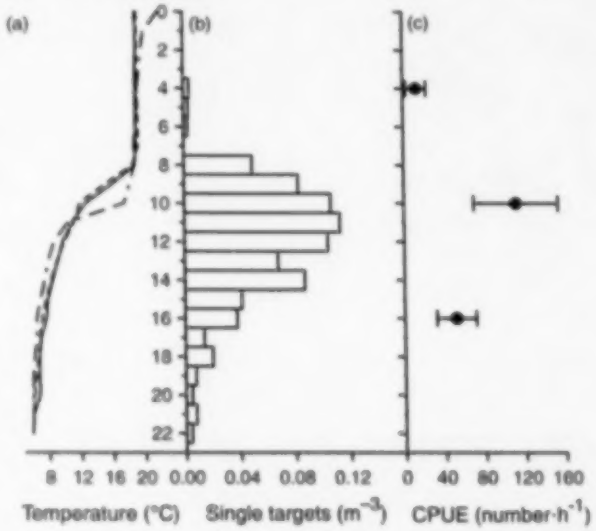
To test whether the mass of prey consumed by herring differed between daytime and nighttime, we conducted a separate single-factor analysis of variance for each season. We used the median stomach contents from each gill net that caught at least six fish as an independent replicate and time (day versus night) as the treatment. Parametric assumptions were confirmed by a Bartlett's homogeneity of variance test and a normal plot of residuals (Zar 1999).

If the herring respond to prey concentrations in their habitat, we predict that there will be an association between the mass of food in the stomachs and the concentration of zooplankton in the water column. We conducted separate ANCOVAs for the daytime and nighttime data. For each ANCOVA, the dependent variable was the median stomach contents in a gill net, the treatment was the period (May, July, October), and the covariate was the zooplankton concentration in the water column adjacent to the gill nets.

Prey consumption by herring in relation to school size

We assumed that there was a direct relation between the size of a herring school and the number of fish captured when the school encountered a gill net. For this assumption to be reasonable, schools must fit within the area of the gill nets used, and the length:height ratio of schools must be fixed (otherwise schools with the same number of fish could intersect nets differently). We confirmed these assertions by regressing school height on length using the 136 daytime herring schools identified by the School Detection Module in the EchoView® software, and compared school dimensions with gillnet dimensions (see Results). To quantify the relation between school size and mass of prey consumed, we regressed the median stomach contents of 10 fish randomly selected from a gill net (or all fish if there were fewer than 10) against the number of fish in a gill net. Using all fish in the nets avoids the need to make subjective decisions about the boundaries of individual schools, given the range of spatial patterns found in the nets, thus making ours a conservative test.

Fig. 1. Comparison of acoustic and gillnet estimates of lake herring (*Coregonus artedi*) abundance in relation to water temperature during nighttime sampling in July. The acoustic data (*b*) are single-target counts of herring-sized objects at various depths over an 891-m long transect through the gillnet sampling area from 2225 to 2247 on 11 July 1999. The gillnet data (*c*) are given as catch per unit effort (CPUE); mean ± standard error) for herring caught in all nets set during the nights of 11–13 July 1999 and temperature profiles (*a*) were taken during the day or night on the same dates.



Results

Schooling behaviour of herring

There is good agreement between hydroacoustic and gillnet estimates of herring abundance in the water column (Fig. 1). Acoustic data are most accurate below approximately 5 m and the data indicate a continuous range of single acoustic targets in the herring target strength range. The only fish caught by the corresponding gill net were herring, and the catches per hour at 10 and 16 m are in roughly the same ratio as the abundances of acoustic targets at these depths (Fig. 1). In a similar October comparison, acoustic and gillnet estimates both indicate that fish are abundant at 16 m, but other net sets were at depths too shallow for reliable comparison with acoustic data. In May the gillnet estimates indicated that all fish were in shallow water and none were at 16 m, and although the acoustic estimates are not reliable at the shallow depths, they do indicate no fish at 16 m. As in July, the only fish caught by gill nets in May and October were herring. We take these observations to be a strong

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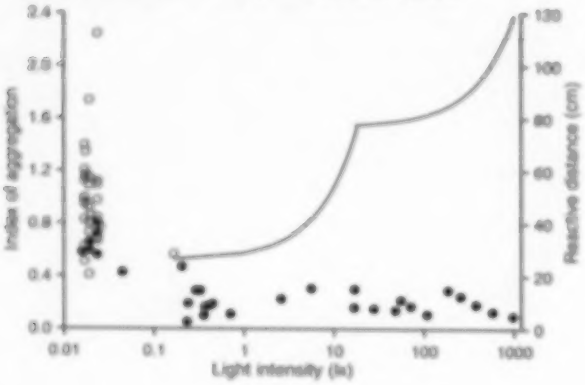
Fig. 2. Indices of aggregation (IA) for lake herring in the gill nets in relation to light intensity. Each point represents a single net catch of at least seven fish. Solid circles represent gill nets in which the IA was statistically different from random and open circles represent gill nets in which the aggregation was random. The reactive distances for lake trout (*Salvelinus namaycush*) from Vogel and Beauchamp (1999) are also plotted.



indication that hydroacoustic and gillnet estimates of fish abundance show good agreement and that our single target strength criterion of –47 to –37 dB corresponds to herring.

Spatial analyses of gillnet catches indicated that fish were typically spread out from one another during the night but formed schools during the day (Fig. 2). At light levels above 0.04 lx, the IA was statistically different ($p < 0.05$) from random in all instances and indicated that fish were aggregated at the scale of the gill net. At light levels below 0.04 lx, 82% of the IAs were statistically indistinguishable from random. These observations suggest that herring schools form or break up at a threshold light intensity, and this is confirmed by repeated acoustic observations of school dissipation indicating that this phenomenon occurs predictably at dusk and that it happens quite quickly (S.W. Milne, unpublished data). Our data suggest that this light threshold is at or near 0.04 lx, which is much greater than for other similar-sized species — 0.000 03 lx for *Engraulis mordax* (Hunter and Nicholl 1985) and 0.000 011 lx for *Trachurus symmetricus* (Hunter 1968). A model of lake trout reactive distance (Vogel and Beauchamp 1999) dependent on light intensity and turbidity (average turbidity for Lake Opeongo is 1.17 nephelometric turbidity units; A. Skinner, Ontario Ministry of Natural Resources, 300 Water Street, Peterborough, ON K9J 8M5, personal communication) indicates that the visual acuity of lake trout, which feed intensively on herring, does increase rapidly as light intensity goes up. However, this increase does not begin until around 4 lx (Fig. 2), two orders of magnitude higher than the threshold intensity for herring schooling (approximately 0.04 lx; Fig. 2). Furthermore, during the day (surface light intensity >319 lx), when herring form schools, lake trout swim faster than they do at night (<0.4 lx; Kruskal–Wallis test, $\chi^2 = 64.2$, $p < 0.0001$), but this increase in swimming speed does not occur until light intensities are much higher than those that evoke schooling (Fig. 3) and intensities are similar to those that permit a rapid increase in reactive distance according to the Vogel–Beauchamp model (Fig. 2).

Fig. 3. Displacement rates of adult lake trout fitted with ultrasonic tags in relation to light intensity at the lake surface. Each point on the graph is the average displacement rate for all individual fish detected during a tracking session. The plotted line is a transformed linear regression fitted to displacement rate versus log light intensity.

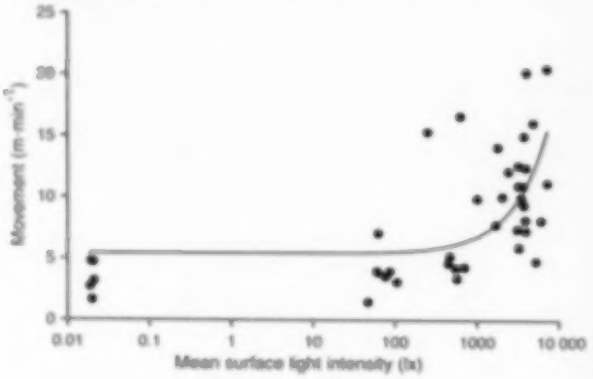
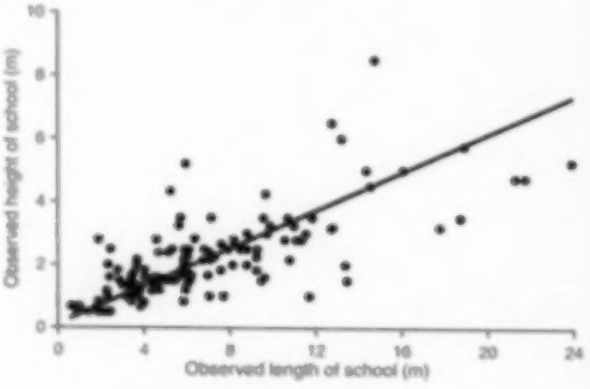


Fig. 4. The sizes of lake herring schools determined from EchoView® School Detection Module analyses of daytime acoustic data from all sampling seasons. Median length and height of the schools are 5.8 and 1.8 m, respectively. The slope of the geometric mean regression (plotted line) is 0.30 with an intercept of 0.12.



Acoustic measurements of herring school size across all sampling seasons indicate that school height increases with length (Fig. 4). A geometric mean regression (Sokal and Rohlf 1995) fitted to these data passes very close to the origin (intercept = 0.12) indicating a fixed height:length ratio for all schools regardless of size (slope = 0.30). This indicates that schools are roughly circular disks and we assume that they are elliptical in cross section. Noting that median school length and height are 5.8 and 1.8 m, respectively, the cross-sectional area of the median size of a school that encounters a gill net would be 8.2 m^2. Gillnet sets were 45 m long and 2.2 m high so that the median-sized herring school would occupy 8.3% of a gill net. The majority of schools (81%) were less than 10 m long and would individually occupy less than 24% of the net area, assuming the elliptical model with an aspect ratio of 0.3. These observations indi-

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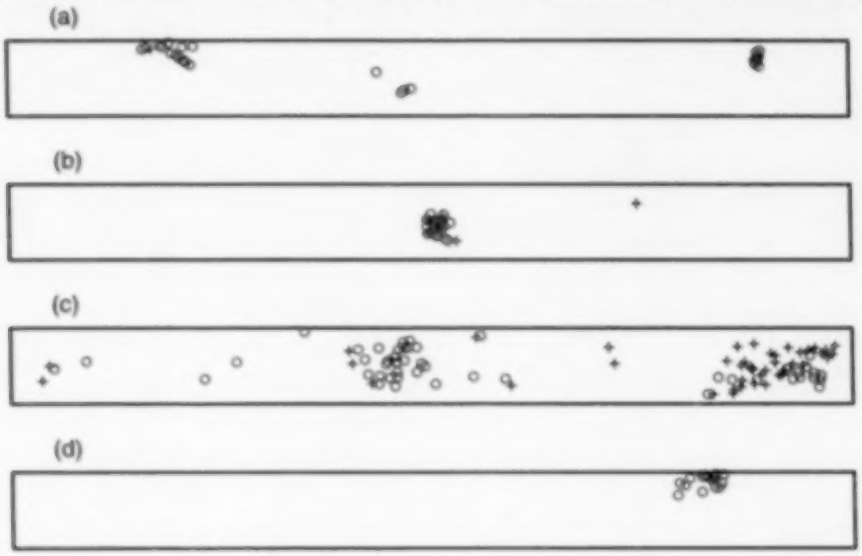
Fig. 5. Patterns of lake herring distributions from selected daytime gillnet sets. The rectangles represent the 45 m × 2.2 m dimensions of the gillnet sets (not to scale). Each symbol represents a single fish, and + and ○ indicate opposite directions of travel upon encounter with the net; *a* and *b* show data from individual net sets from May, *c* shows data from July, and *d* shows data from October.

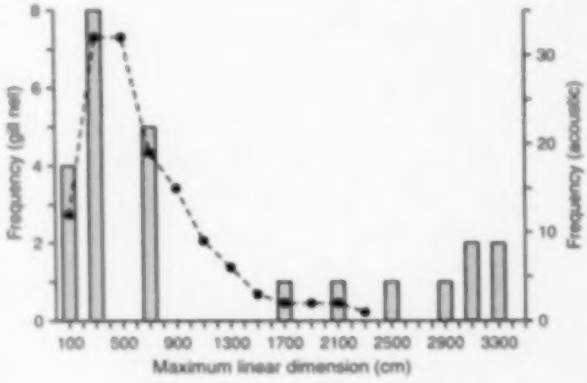


cate that the majority of herring schools would be entirely captured within the gill nets we used.

We observed a wide variety of patchy distributions of herring in daytime gillnet sets (Fig. 5). Multiple schools varying in size were caught in some nets (Fig. 5*a*), while in others it appeared as if a single school was captured entirely within the net (Fig. 5*b*). School boundaries were more difficult to define in some instances (Fig. 5*c*), whereas in others only a part of a school may have been captured (Fig. 5*d*). Some schools consisted entirely of fish travelling in the same direction at the time of capture (Fig. 5*d*), whereas others contained fish travelling in opposite directions (Fig. 5*c*). As described in Methods, we consider any distinct aggregation of fish, regardless of travel direction, to be a single school. Our net sets were of short duration (mean of 31 min) and a high proportion of the 63 daytime sets caught fewer than seven or no fish (38 sets, or 60% of the total). This indicates low herring concentrations relative to the sampling area of the nets and hence a very small chance that two schools coming from opposite directions would encounter the net at the same place.

There is good agreement between the length of herring schools measured acoustically and the length of those measured in the gill nets (Fig. 6). The number of schools measured in gill nets (25) was much lower than the number measured acoustically (135), but the distributions of maximum linear dimensions were very similar, with the most frequent school lengths ranging from approximately 100 to 800 cm (68% of all gillnet schools and 70% of all acoustic schools). The largest school measured acoustically was 2300 cm long, but there were six "schools" from gill nets that were longer — up to 3300 cm. However, in all six instances there was more than one clump of fish in the gill net (e.g., Figs. 5*a* and 5*c*), so these are actually overestimates of school size. Had it been objectively possible to measure these clumps individually, the right tail of the gillnet distribution would have ended up much closer to the main size mode (Fig. 6). In general, herring schools range in length from roughly 100 to 2300 cm, the majority being shorter than approximately 1000 cm (Fig. 6).

Fig. 6. Frequency distribution of lengths of lake herring schools in each of the 25 daytime gillnet sets. A distribution of the lengths of daytime schools from acoustic analysis is superimposed.



Diel patterns in herring stomach contents

Stomach contents of herring consisted primarily of zooplankton with rare occurrences of chironomid pupae in the spring night samples. Results indicate that the stomachs of herring captured during the day contained more prey than those captured at night during the May (analysis of variance, $F_{[1,10]} = 28.96$, $p < 0.001$) sampling period. This trend also existed for July ($F_{[1,8]} = 0.91$, $p = 0.37$) and October ($F_{[1,10]} = 1.13$, $p = 0.31$) but was not statistically significant. A meta-analysis based on combining the probabilities from

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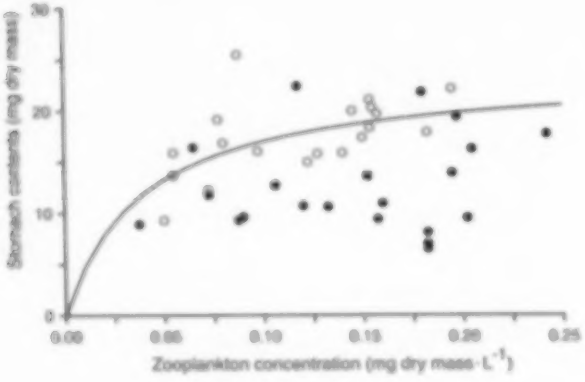
Fig. 7. Relationship between median stomach contents and the zooplankton concentration in the water column for day (○) and night (●). For the daytime data the statistically significant association between variables is summarized using a simple saturation curve forced through the origin:

$$Y = \frac{23.8(3.3)X}{0.04(0.02) + X}, \quad r^2 = 0.67$$

where Y is median stomach contents, X is zooplankton concentration, and r^2 is explained variation, and mean coefficients (with standard errors) are shown. No statistical relationship exists for the nighttime data.



these three independent tests (Sokal and Rohlf 1995) supports the overall conclusion that herring consume more food during the day than at night ($p = 0.0006$). Stomach-clearance simulations based on evacuation-rate models for other cold-water species such as sockeye salmon (*Oncorhynchus nerka*), coho salmon (*Oncorhynchus kisutch*), and rainbow trout (*Oncorhynchus mykiss*; He and Wurtsbaugh 1993) are consistent with the hypothesis that nighttime feeding is minimal and that nighttime stomach contents consist of remains of prey consumed during the day.

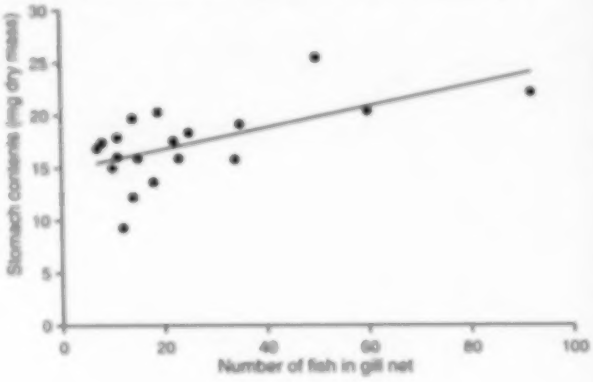
Stomach contents in relation to available prey

Analyses of daytime patterns in median stomach contents among sampling periods using zooplankton concentration in the water column as a covariate indicated a strong effect of zooplankton concentration (ANCOVA, $F_{[1,15]} = 9.7$, $p = 0.007$) that is similar across sampling periods ($F_{[2,15]} = 1.4$, $p = 0.28$). Slopes of the stomach contents – zooplankton concentration regressions were homogeneous across sampling periods (ANCOVA, $F_{[2,13]} = 0.19$, $p = 0.83$). A parallel analysis of the nighttime data indicated no effect of zooplankton concentration (ANCOVA, $F_{[1,17]} = 3.1$, $p = 0.1$). Combining data across all periods (Fig. 7) indicates a relationship between our index of daytime herring consumption and zooplankton concentration, while at night no such relationship is evident.

Prey consumed in relation to school size

On the basis of the fixed aspect ratio for herring schools (Fig. 4) and the fact that most schools fit well within the area of a gill net, we considered the number of fish found in a gill net to be directly related to the number of fish in the school that encountered the net. This measure of school size was related to the mass of prey found in the stomachs of fish within the school (Fig. 8) and indicated that fish in large schools have fuller stomachs than those in small schools.

Fig. 8. Relationship between lake herring stomach contents and the number of fish captured in a gill net. Each point is the median stomach contents of 10 randomly sampled fish (or all fish if fewer than 10 were caught) from daytime gillnet catches. The least squares linear regression is shown: $Y = 14.7 + 0.1X$, $r^2 = 0.37$, $p < 0.001$, where Y is stomach contents, X is the number of fish in the school, r^2 is the explained variance, and p is the probability associated with the statistical test of linearity.



Discussion

Our observations are consistent with the hypothesis that lake herring form schools at daybreak as light intensity increases in the water column. This overall trend is expected because vision is the primary sense used by fish to maintain schools (Whitney 1969; Bohl 1980; Partridge and Pitcher 1980), although some evidence suggests that chemical and olfactory cues may also be important (Krause 1993). Bohl (1980) suggested, specifically for herring, that light levels at night are simply too low for them to visually maintain contact with schooling neighbours.

Given that herring form schools, what are the ecological forces that make schooling behaviour advantageous? Our data suggest that schooling increases feeding efficiency for herring, an additional benefit to the increase in predator-avoidance abilities that is typically the product of schooling behaviour. If schooling were primarily a predation-defence mechanism (Magurran et al. 1985; Turner and Pitcher 1986) for herring in Lake Opeongo, we would expect their schools to disperse when light levels fall to those at which the visual acuity of lake trout, their primary predator, is reduced.

However, our data indicated that herring continue to school at light levels well below those predicted by Vogel and Beauchamp's (1999) reaction-distance model for lake trout. Our tracking data for lake trout also show that lake trout movement decreases greatly at night and that this decrease occurs at light intensities greater than those required to evoke school dispersal. These observations suggest that there must be advantages to schooling in addition to simple

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predator avoidance, and that herring persist in schools when predation risk is low.

What advantage is there for herring to remain in schools even when it is too dark for their predators to see them? We observed that herring stomachs are fuller during the day than at night. We also observed that the mass of prey in stomachs increases with prey abundance during the day but there is no such association at night. These observations demonstrate that schooling herring forage more efficiently during the day than individual herring feeding singly at night. They also raise the possibility that herring may even derive a feeding benefit from schooling. This is supported by our observation that individual herring from large schools had more prey in their stomachs than those from small schools. Similar observations have been made for other fish species (Pitcher and Magurran 1983; Morgan 1988; Ranta and Kaitala 1991) and it has also been noted that individual schooling fish have greater growth rates than solitary ones, possibly as a result of higher food-assimilation efficiency in the absence of isolation stress (Davis and Olla 1992; Peuhkuri et al. 1995).

Social facilitation may account for this pattern of increased per-capita foraging success in schools — the willingness of any individual to feed increases with the number of other individuals feeding (Baird et al. 1991; Ryer and Olla 1992). Alternatively, the corporate vigilance, or many-eyes, hypothesis has been proposed: as school size increases, individual fish need to spend less time being alert to predators and can thus devote more time to feeding (Bertram 1978; Morgan 1988). The many-eyes hypothesis also predicts that the effective reaction distance of a school will grow with the school diameter, hence greatly augmenting the ability of individual fish to locate patchy food resources (Pitcher et al. 1982; Baird et al. 1991; Ryer and Olla 1992). Our observation that herring schools in Lake Opeongo vary widely in length (the majority fall between approximately 300 and 1000 cm but some were as long as 2300 cm) even though large schools appear to offer a significant advantage to their members is consistent with the "optimal group size" ideas of Parrish and Edelstein-Keshet (1999). These authors point out that because many costs and benefits are associated with variation in school size (e.g., small schools offer little defence against predators, while very large schools can be easily detected by predators and individual school members may be resource-limited as a result of intraspecific competition), one would expect the optimal group size to fluctuate seasonally, daily, or hourly depending on predation pressure, food-patch size, individual hunger, and breeding stage.

Acknowledgements

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Interacting effects of behavior and oceanography on growth in salmonids with examples for coho salmon (*Oncorhynchus kisutch*)

Melissa L. Snover, George M. Watters, and Marc Mangel

Abstract: Positive and negative relationships between pre- and post-smolt growth rates in salmonids have been observed, but the mechanisms underlying these relationships are not understood. We hypothesize that growth at sea is controlled by interactions between behavior and ocean conditions and that no one relationship is correct. We present a growth model with habitat-specific rates of anabolism that allow resource acquisition to vary in response to the behavior–environment interaction. Our model predicts positive relationships between pre- and post-smolt growth rates when ocean resources have clumped, defensible distributions under which conditions that aggressive behaviors facilitate increased access to those resources. Negative relationships are predicted when resources are dispersed and aggressive behaviors are ineffective. We present data relating pre- and post-smolt growth rates for more than 15 stocks of coho salmon (*Oncorhynchus kisutch*). These data indicate that shortly after out-migrating, aggressive behaviors are not effective for securing resources in the ocean (i.e., there are negative or no relationships between pre- and post-smolt growth rates). As coho spend more time at sea, however, variability in environmental conditions can elicit a variety of growth responses.

Résumé : Il est possible d'observer des relations positives et des relations négatives entre la croissance des présaumoneaux et celle des postsomoneaux, mais les mécanismes sous-jacents à ces relations ne sont pas connus. Nous posons en hypothèse que la croissance en mer est contrôlée par les interactions entre le comportement et les conditions océaniques et qu'aucune relation particulière n'est la bonne. Nous présentons un modèle de croissance avec des taux d'anabolisme spécifiques aux habitats qui permet à l'acquisition de ressources de varier en fonction de l'interaction comportement environnement. Notre modèle prédit des relations positives entre les taux de croissance des présaumoneaux et des postsaumoneaux lorsque les ressources océaniques ont des répartitions contagieuses et défendables et que les comportements d'agressivité facilitent un accès accru à ces ressources. Il prédit des relations négatives lorsque les ressources sont dispersées et que les comportements agressifs sont inefficaces. Nous présentons des données qui mettent en relation les taux de croissance des présaumoneaux et des postsaumoneaux chez 15 stocks de saumons coho (*Oncorhynchus kisutch*). Ces données indiquent que, peu après l'émigration vers l'océan, les comportements agressifs ne sont pas efficaces pour procurer les ressources océaniques (c.-à-d., les relations entre les taux de croissance des présaumoneaux et des postsaumoneaux sont négatives ou nulles). À mesure que les saumons coho passent plus de temps en mer, la variabilité des conditions du milieu peut provoquer une variété de réponses de croissance.

[Traduit par la Rédaction]

Introduction

The link between individual growth rates and age at maturity in salmonids is well established (e.g., Skilbrei 1989; Nicieza and Braña 1993), but conflict exists regarding the relationship between freshwater and salt-water growth performance. When smolt age is controlled for, positive relationships between smolt length and subsequent growth in salt water have been found for Atlantic salmon (*Salmo salar*; Skilbrei 1989; Friedland and Haas 1996), Chinook salmon (*Oncorhynchus tshawytscha*; Heath et al. 1996), and steelhead trout (*Oncorhynchus mykiss*; Johnsson et al. 1997). Negative relationships have been found for Atlantic salmon (Nicieza and Braña 1993) and coho salmon (*Oncorhynchus*

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kisutch; Johnsson et al. 1997). Even the absence of such a relationship has been found for Atlantic salmon (Nicieza and Braña 1993). The strengths and signs of these correlations are important at the population level because fast-growing fish typically mature at younger ages and smaller sizes. To our knowledge, this conflict has yet to be resolved.

In fresh water, links have been found between behavior and growth rates. Studies of Atlantic salmon have shown that fry with high standard metabolic rates rank high in dominance status and have higher growth rates (Huntingford et al. 1990; Metcalfe et al. 1995). Wild coho salmon parr with high dominance status defend territories, acquire more resources, and grow faster than less dominant individuals (Puckett and Dill 1985; Nielsen 1992; Martel 1996). Ultimately, dominant individuals have the potential to be the longest smolts (Martel 1996).

In salt water, the relationship between behavior and growth rate is less obvious. Aggressive behaviors in coho salmon may remain after the smolt transformation and possibly result in dispersed distributions at sea (Paszkowski and Olla 1985; Jaenicke and Celewycz 1994), but other species of Pacific salmon are more aggregated during their ocean residence (e.g., Jaenicke and Celewycz 1994; McKinnell et al. 1997). Ultimately, growth rates at sea will depend on behavior and its interaction with resource distribution (e.g., Paszkowski and Olla 1985; Martin-Smith and Armstrong 2002; Vøllestad and Quinn 2003).

Here, we illustrate how the conflicting relationships between freshwater and salt-water growth rates of salmonids can be explained by a growth model that parameterizes the behavior–environment interaction. We show how the effectiveness of aggressive behaviors for food acquisition and growth can vary both with environmental conditions in the ocean and with fish length. When environmental conditions cause resources to be relatively well mixed, energy expended through aggressive behaviors will lead to decreased growth rates; the reverse is predicted when environmental conditions cause resources to be clumped. We illustrate these interactions by constructing a growth model for coho salmon. We present data that provide information on the relationships between freshwater and salt-water growth performance of coho from British Columbia, Washington, Oregon, and California. We compare predictions from our model to these data and make inferences about how aggressive behaviors and resource distribution interact to influence growth at sea.

Materials and methods

The von Bertalanffy growth function (VBGF)

The metabolic growth model refined by von Bertalanffy (1938) describes changes in body mass (dW/dt) from the difference between anabolism (energy gain) and catabolism (energy loss):

$$(1) \qquad \frac{dW}{dt} = HW^m - cW^n$$

where W is body mass; t is time; H is the coefficient of anabolism; and c is the coefficient of catabolism. The exponents m and n respectively describe the allometric scaling of energy gain and loss.

We reformulated eq. 1 in terms of length (L) by assuming that the length–mass relationship is described by $W = L^3$; $m = 2/3$; and $n = 1$:

$$(2) \qquad \frac{dL}{dt} = E - kL$$

where E is a rescaled coefficient of anabolism, and $E = H/3$. Similarly, k is a rescaled coefficient of catabolism, and $k = c/3$. The assumption that $m = 2/3$ is based on the idea that anabolism scales with surface area. Essington et al. (2001) estimated m for a variety of marine and freshwater fishes, and almost half of the estimates fell between 0.65 and 0.85. Essington et al. (2001) estimated a mean m of 0.77. Qualitative predictions from eq. 1 are robust to changes in m over the range (0.65, 0.85), and for mathematical convenience, we used the convention $m = 2/3$. The assumption that $n = 1$ is based on the idea that catabolism scales with volume; Essington et al. (2001) found that this convention is reasonable.

Integrating eq. 2 identifies the more common, mathematical interpretation of k as a growth coefficient describing the rate at which a fish approaches its asymptotic size. The solution of eq. 2 is

$$(3) \qquad L_t = L_\infty - (L_\infty - L_0)e^{-kt}$$

where L_t is length at time t, and L_0 is the initial length. L_∞ is the asymptotic size at which the growth rate is zero. From eq. 2, L_∞ can be described as

$$(4) \qquad L_\infty = \frac{E}{k}$$

Although the dual interpretations of k seem confusing (i.e., a rate of catabolism in eq. 2 and a growth coefficient in eq. 3), a biological argument can be constructed to suggest that an individual's rate of energy loss may be functionally related to its rate of energy gain. E is related directly to the amount of resources available to an individual and will vary with environmental conditions and individual behavior. Higher levels of k equate to higher metabolic rates (von Bertalanffy 1938; Beverton and Holt 1959), and standard metabolic rates can be positively correlated with dominance behavior (e.g., Metcalfe et al. 1995). The effectiveness of aggressive behaviors associated with dominance status in securing more resources will depend on how environmental conditions distribute those resources in time and space (Martin-Smith and Armstrong 2002). When environmental conditions facilitate the defense of feeding territories by dominant individuals, those individuals may be able to sequester more resources and achieve increased levels of E. Under these conditions, E may be positively related to k. When conditions do not facilitate increased food acquisition by dominant individuals, E may be the same for all individuals. Under these conditions, E may be independent of k, and from eq. 2, individuals with a higher k will grow slower because they acquire the same amount of resources but have higher metabolic demands. Considering the two scenarios described here, it seems logical to describe energy gain as a function of energy loss. We explicitly accounted for such behavioral and environmental effects on growth by parameterizing E as a function of k:

$$(5) \qquad E = \gamma k^{\psi}$$

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where γ and ψ respectively determine the degrees to which E depends on environmental and behavioral factors, and $0 \leq \psi \leq 1$.

When ψ is close to 1, dominant behaviors associated with k are effective for sequestering resources from the environment. When ψ is close to 0, an individual's ability to sequester resources from the environment is controlled mostly by the environment itself. Limnologic and oceanographic processes can influence the value of ψ by making resources more or less clumped; the distribution of resources ultimately influences both their accessibility and defensibility by fishes. Similarly, growth itself can influence the value of ψ; larger fish may have increased access to resources. Extreme parameterizations of E can be made by setting $\psi = 1$ (i.e., E is only determined by behavioral factors related to k) or $\psi = 0$ (i.e., E is only determined by environmental conditions). Salmonids will have at least two Es, one for fresh water and one for salt water, although there may be multiple Es for the different salt-water growth stanzas.

Application of the VBGF to coho salmon

We described the growth of coho salmon during three stanzas (one stanza in fresh water and two stanzas in salt water) that approximate Sandercock's (1991) description of the dominant life cycle of these fish. After emergence from the gravel, growth in fresh water occurs for 12 months. We assumed that the smolt transformation occurs in month 12, and growth in salt water occurs while coho are 13–30 months old. Fish that mature early spend 6 months at sea; they experience zero sea winters and one growing season. Fish that mature late experience one sea winter and two growing seasons while spending 18 months at sea. The three growth stanzas are temporally separated by the smolt transformation and the sea winter between early and late maturation; the three stanzas are also differentiated by shifts in E.

For growth in fresh water, we considered only an extreme parameterization of anabolism. We assumed that an individual's k is determined prior to its emergence from the gravel and that k is constant throughout its life. Thus, the length of an individual at some time after its emergence from the gravel is conditioned on k, which again is directly related to metabolic rate (von Bertalanffy 1938; Beverton and Holt 1959) and indirectly related to dominance behavior (Metcalfe et al. 1995). Since the freshwater environment is heterogeneous and dominant coho parr (large individuals with higher values of k) are more able to secure food resources (Puckett and Dill 1985; Nielsen 1992; Martel 1996), we applied eq. 5 by assuming that $\psi = 1$ and $\gamma_{FW} > 0$.

$$E_{FW} = \gamma_{FW} k \tag{6}$$

The subscript FW indicates fresh water, and considering eq. 4, γ_{FW} is equal to the maximum length at smolt transformation. Growth through the freshwater stanza is described by substitution from eqs. 4 and 6 into eq. 3.

$$L_{FW}(t|k) = \gamma_{FW} - (\gamma_{FW} - L_f)e^{-kt} \tag{7}$$

L_f is the length of a postemergent fry, and t is time (months) since emergence from the gravel. This parameterization of E_{FW} predicts a positive relationship between smolt length and k (e.g., Fig. 1).

For anabolism at sea, we used the general approach described by eq. 5.

$$E_{SW} = \gamma_{SW} k^{\psi} \tag{8}$$

The subscript SW identifies salt water; $\gamma_{SW} \geq 0$; and $0 \leq \psi \leq 1$. We explored 5 alternatives: (*i*) aggressive behaviors associated with k are heldover from fresh water and increase access to resources in salt water, regardless of environmental conditions ($\gamma_{SW} > 0$ and $\psi = 1$), (*ii*) anabolism in salt water is entirely determined by environmental conditions ($\gamma_{SW} > 0$ and $\psi = 0$), and (*iii–v*) $\psi = 0.75$, 0.5, or 0.25, and $\gamma_{SW} > 0$. We constrained all five alternatives by assuming that the expected value of E_{SW} is greater than the expected value of E_{FW} and that $E_{SW} \geq kL$. The first constraint acknowledges that a primary mechanism for the evolution of anadromy in salmonids is increased food availability at sea. Such an increase presumably allows for increased adult size and fecundity (Gross et al. 1988). The second constraint ensures non-negative growth rates. Regardless of how we characterized E_{SW}, we assumed that an individual's length after the smolt transformation remains conditioned on k.

$$L_{SW}(t|k) = \begin{cases} \dfrac{E_{SW,1}}{k} - \left(\dfrac{E_{SW,1}}{k} - L_{FW}(12|k)\right)e^{-k(t-12)} & \text{for } 13 \leq t \leq 23 \\ \dfrac{E_{SW,2}}{k} - \left(\dfrac{E_{SW,2}}{k} - L_{SW}(23|k)\right)e^{-k(t-23)} & \text{for } 24 \leq t \leq 30 \end{cases} \tag{9}$$

Initial length for growth during the first salt-water stanza, $L_{FW}(12|k)$, is the length at the smolt transformation. Initial length for growth during the second salt-water stanza, $L_{SW}(23|k)$, is the length at the start of the second growing season. E_{SW} is further subscripted by 1 and 2 to indicate the number of growing seasons that an individual experiences at sea.

Net salt-water growth of coho

We used information from Shapovalov and Taft (1954) to obtain reasonable values for the parameters in eqs. 6–9 and simulate representative growth trajectories for coho. Note that we did not fit our growth model to the data provided by Shapovalov and Taft (1954); our intention was to describe growth patterns in general rather than to predict size at age. We fixed L_f (2 cm) and γ_{FW} (18 cm) and treated k as a random variable describing individual and intercohort variation in dominance status and freshwater growth performance. We found that drawing k from a gamma distribution with a mean

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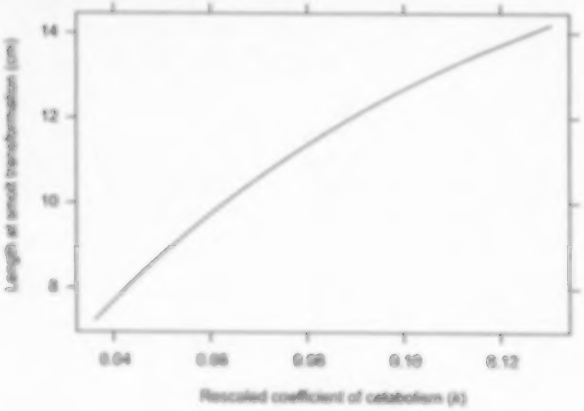
Fig. 1. The relationship between k and smolt length described by eq. 5, where smolt length is measured 12 months after emergence from the gravel.



of 0.07 and coefficient of variation (CV) equal to 0.30 predicted a distribution of smolt lengths (individuals within a cohort) that was consistent with those observed by Shapovalov and Taft (1954). Thus, we simulated intercohort variation in freshwater growth by randomly drawing mean levels of k from a normal distribution with mean of 0.07 and standard deviation (SD) of 0.01. Within cohorts, we then drew individual values of k from gamma distributions around the cohort-specific mean values of k with a fixed CV (0.30).

Each individual's k was carried over to the salt-water growth stanzas. To describe growth during the two salt-water stanzas and simulate intercohort variation in anabolism at sea, we drew $E_{SW,1}$ and $E_{SW,2}$ from random normal distributions with means of 6.4 and SDs of 0.5. We considered the five previously described formulations of E_{SW} to predict lengths at 13–30 months after smolt transformation. For each cohort and each parameterization of E_{SW}, we drew $E_{SW,1}$ and $E_{SW,2}$, set $k = 0.07$, and set $\psi = 1$, 0.75, 0.5, 0.25, or 0. We then solved for γ_{SW} in eq. 8 (one solution each for $E_{SW,1}$ and $E_{SW,2}$). The net growth of each individual was estimated as $L(181k) - L(121k)$ for fish that mature early and spend zero winters at sea or $L(301k) - L(121k)$ for fish that mature late and spend one winter at sea. We simulated the growth of 100 individuals from each of 50 cohorts using the five parameterizations of E_{SW}.

We computed cohort-specific estimates of mean net growth and plotted these against cohort-specific estimates of mean smolt length. We used cohort-level summary statistics because the empirical data we have to compare with our model output is primarily in the form of annual averages for smolt length and for adult return lengths.

Data on coho salmon

We compared predictions from our model of coho growth to observations on the relationship between smolt length (an index of growth performance in fresh water) and net growth after one growing season (i.e., zero sea winters) and after two growing seasons (i.e., one sea winter). We made comparisons with observational data from the Coded Wire Tag (CWT) database (http://www.rmis.org), literature sources, and the University of Washington Hatchery (data provided by A. Vøllestad and T. Quinn, Aquatic and Fisheries Sciences, University of Washington, Seattle, WA 98195, USA; Quinn et al. 2004 and Vøllestad et al. 2004 presented these same data in a different manner). We ensured that all the observational data from each source represented fish that smolted at one age (i.e., observations on age 0+ and age 1+ smolts were not mixed); this allowed us to use smolt length as a proxy for freshwater growth performance (e.g., Fig. 1).

The CWT data required extensive preprocessing. We used information on coho that could reasonably be assumed to have outmigrated shortly after release by the hatcheries. We considered only those tag codes representing releases of age 1+ smolts and in which the month of release was reported to be within the range March–June for stocks from California and Oregon or April–July for stocks from Washington and British Columbia. We classified release groups as comprising age 1+ smolts when differences between reported release and brood years were equal to two. We also limited our consideration to tag codes for which the average mass of individuals within a release group was within the range 5–50 g. We converted group-specific estimates of average mass at release (w) to estimates of average smolt length (l) with $l = [w/(4.36 \times 10^{-6})]^{0.31}$. The parameters of this equation were estimated by fitting a robust regression model to data on log-release masses and log-release lengths. To fit this model, we combined data from all stocks for which we had such information. We computed return lengths and ages only for fish that were reported to have been captured in terminal fisheries or returned to hatcheries. The numbers of winters that fish spent at sea were computed as differences between reported recovery and release years, but we subtracted a year if fish were recovered during January–March. We computed age- and tag-code-specific estimates of mean length at return. These means were weighted by the estimated number of fish that each length observation (CWT recovery) represented in the total catch.

Many stocks are represented by the CWT data, but we used a three-step protocol to limit the stocks used in our analyses. First, we limited the data to 3 release months as described above. Second, so that release timing within those 3 months would not substantially impact smolt length, we used stock-specific analyses of variance (ANOVAs) to select stocks for which release month explained less than 5.0% of the variation in mean smolt length. Third, of the remaining stocks, we chose the five for which there was the most data. Although we controlled for smolt age and release timing, the CWT data presented here still contains variation arising from cohorts, hatchery influences such as feeding practices, and fish health. We therefore expected the data that successfully passed through our selection protocol to display an overall mean relationship between smolt length and growth performance at sea.

It is likely that individual cohorts will experience different ocean conditions. We addressed this by attempting to control for brood year and observe interannual variability in the relationship between smolt length and growth performance at sea. After applying our data-selection protocol, there were few stocks remaining with enough data to demonstrate such variability. Nevertheless, we selected four stocks from the Columbia River system that retained sufficient data to demonstrate the relationship between smolt

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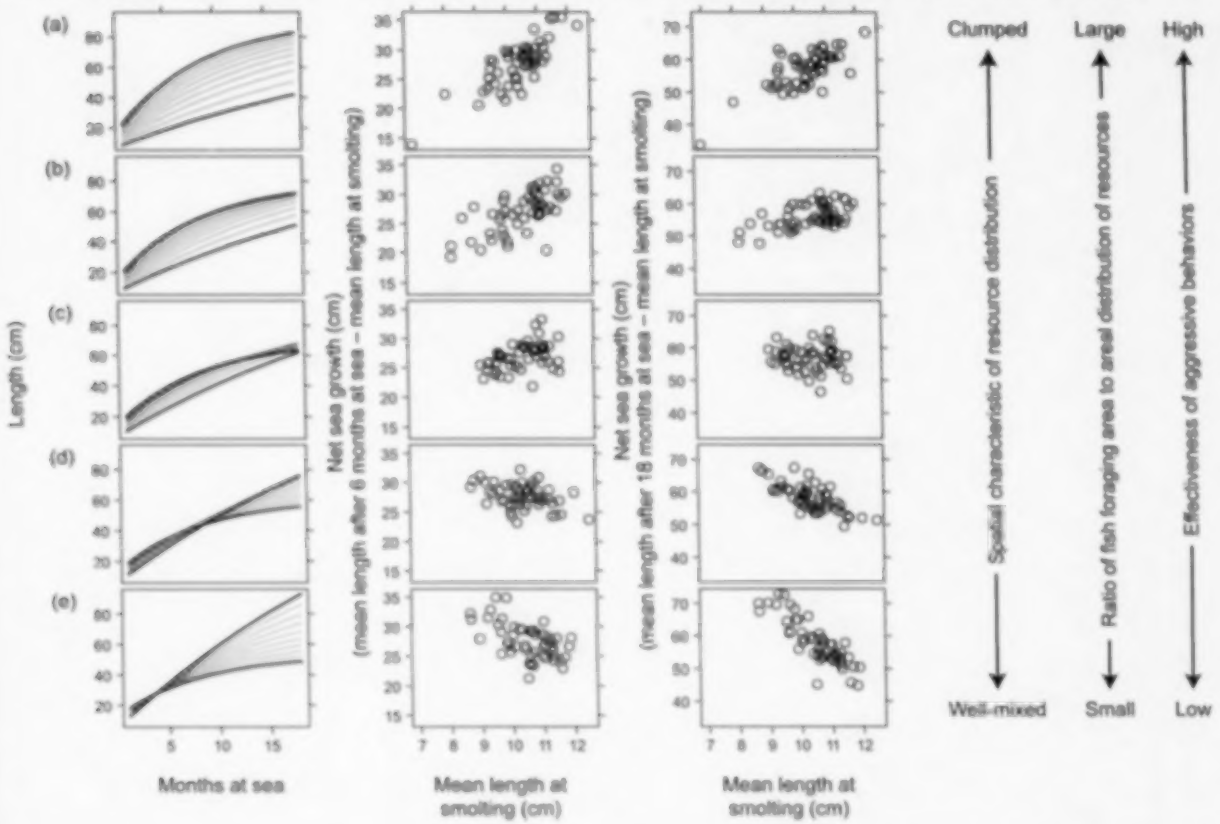
Fig. 2. Predicted growth trajectories from eq. 9. Rows *a*–*e* identify alternative parameterizations of E_{SW}: (*a*) $\psi = 1$; (*b*) $\psi = 0.75$; (*c*) $\psi = 0.5$; (*d*) $\psi = 0.25$; and (*e*) $\psi = 0$. The first column of graphs illustrates simulated, at-sea growth trajectories for 10 individuals with different rescaled coefficient of catabolism (k) values; the bold trajectories identify those individuals that were the largest and smallest smolts. The second column illustrates predicted relationships between smolt length and net growth after 6 months at sea. The third column illustrates predicted relationships between smolt length and net growth after 18 months at sea. In both of these latter columns, each data point represents the mean from a cohort of 100 individuals, and 50 cohorts are illustrated in each panel. On the right side of the figure, schematic scale bars indicate the behavioral and oceanographic interpretations of the parameterizations of E_{SW}.



length and growth performance at sea for 3 separate years within each stock.

It is worth noting that the empirical data presented here represent both hatchery and wild fish and were developed from a variety of methodologies. The CWT data represent 14 hatchery stocks and 1 wild stock and were estimated from mean weights reported in the CWT database. The literature data were from individual measurements of hatchery (Mathews and Ishida 1989; Hager and Noble 1976) and wild (Shapovalov and Taft 1954; Holtby and Healey 1986) coho. Data from two of the literature sources (Holtby and Healey 1986; Mathews and Ishida 1989) were developed by back-calculating lengths from annulus spacing on the scales of individual fish.

Results

Since growth potential at sea is $L_\infty - L(1|k) \sim \gamma_{SW} k^{\psi-1}$, our formulation of E_{SW} had a strong impact on how smolts of varying lengths were predicted to grow in salt water (Fig. 2). Individual growth trajectories converged when $\psi \neq 1$. When $\psi \leq 0.5$, a crossover occurred, and the largest smolts eventually became the smallest individuals. As ψ decreased from 1 to 0, the largest smolts had declining growth potentials at sea, and the reverse was true of the smallest smolts. The age at which individual growth trajectories crossed each other decreased as ψ decreased. When $\psi = 0$, the smallest smolts had substantially greater salt-water growth potential than did the largest smolts, and the crossover occurred soon after the smolt transformation. When $\psi = 1$, the model predicted positive relationships between mean smolt length and mean net growth after both 6 and 18 months at sea. Conversely, when E_{SW} was independent of k (i.e., or $\psi = 0$), the model predicted negative relationships between smolt length and net growth after 6 and 18 months at sea. The transition from a positive to a negative relationship between smolt length and net growth at sea with decreasing ψ was predicted both across individuals (data not shown) and across cohorts (Fig. 2, second and third columns. Note that we illustrate cohort-level predictions in the second and third columns of Fig. 2 for direct comparison to the observational data presented in later figures).

The CWT data demonstrated a range of average relation-

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Fig. 3. Average net growth of coho salmon (*Oncorhynchus kisutch*) released as age 1+ smolts from five hatchery stocks in Oregon. Rows are identified by stock location names recorded in the Coded Wire Tag database: (*a*) Umpqua River (Rock Creek Hatchery), (*b*) Sandy River (Sandy Hatchery), (*c*) Nehalem River North Fork and tributaries, (*d*) Klaskanine River, and (*e*) Clackamas River Early. Circles identify mean length at release and mean growth increments for multiple groups of fish marked with unique tag codes and from different cohorts. Trend lines are loess smooths. Smooth curves were fitted only when there were at least 10 data points in a panel and the range of smolt lengths was at least 10 mm.

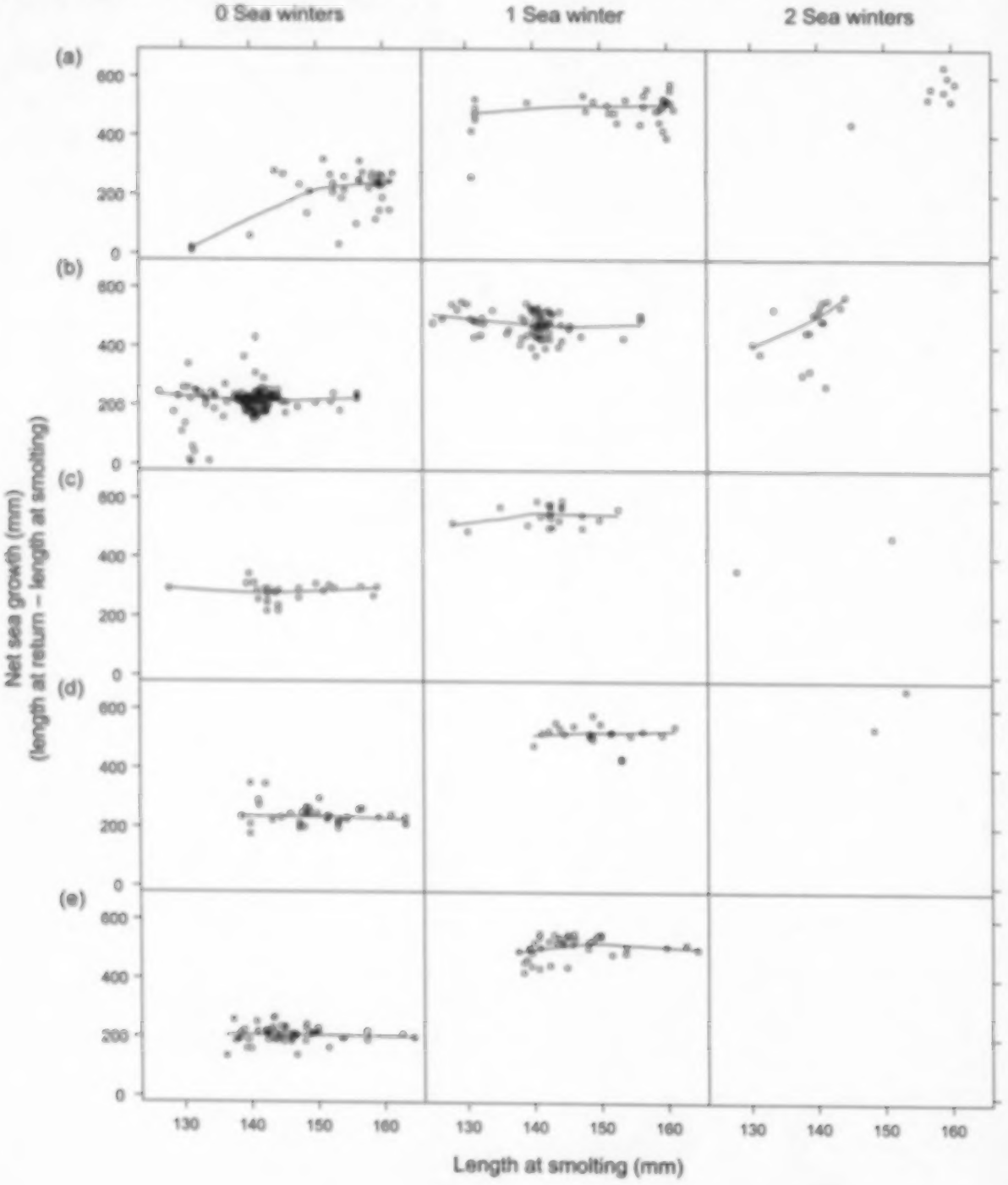

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Fig. 4. Average net growth of coho salmon (*Oncorhynchus kisutch*) released as age 1+ smolts from five hatchery stocks in Washington. Rows are identified by stock location names recorded in the Coded Wire Tag database: (*a*) Lewis River 27.0168, (*b*) Cowlitz River 26.002, (*c*) Cook Creek 21.0429, (*d*) Big Soos Creek 09.0072, and (*e*) Big Quilcene 17.0012. Circles identify mean length at release and mean growth increments for multiple groups of fish marked with unique tag codes and from different cohorts. Trend lines are loess smooths. Smooth curves were fitted only when there were at least 10 data points in a panel and the range of smolt lengths was at least 10 mm.

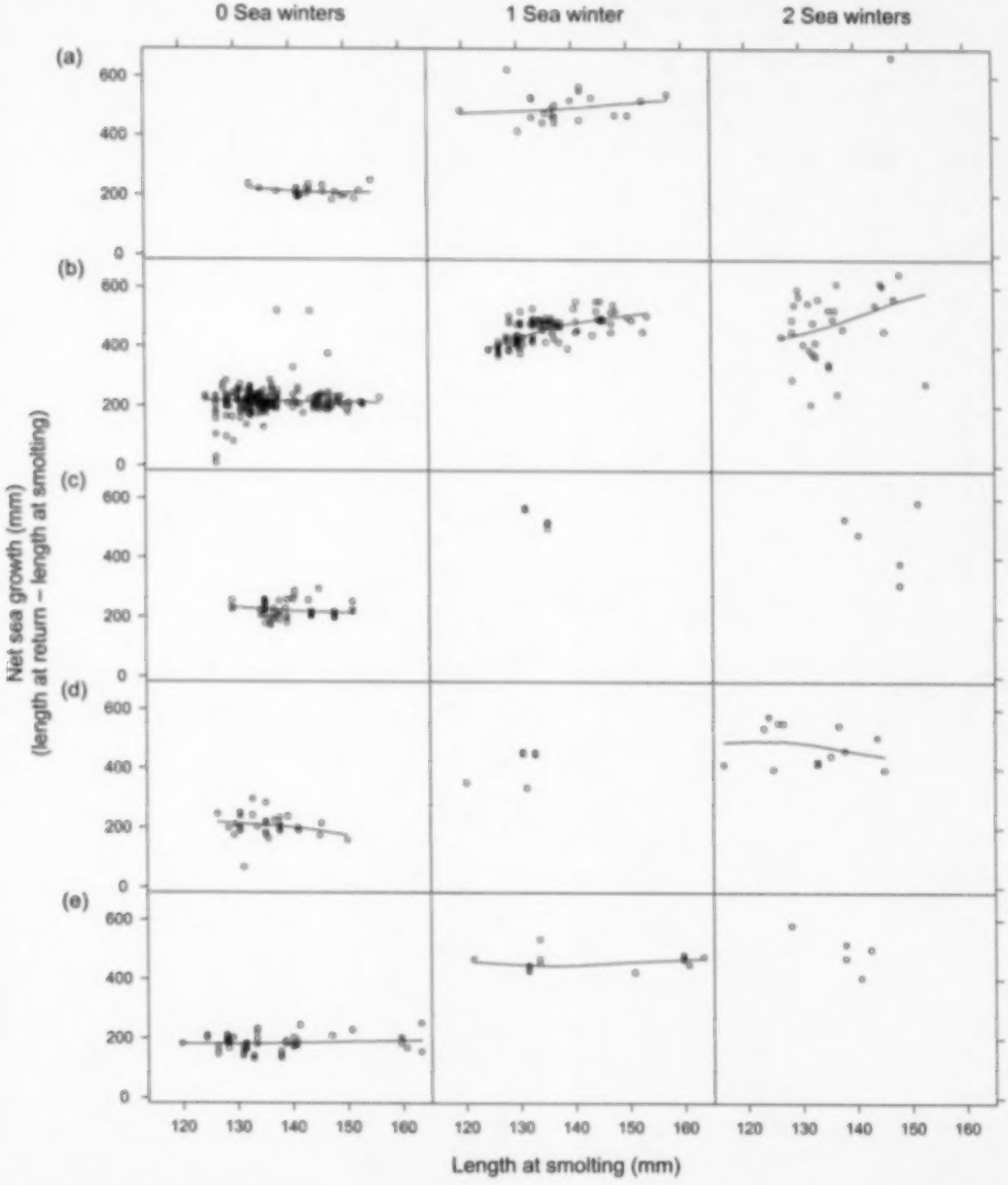

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Fig. 5. Average net growth of coho salmon (*Oncorhynchus kisutch*) released as age 1+ smolts from five stocks in British Columbia. Rows are identified by stock location names recorded in the Coded Wire Tag database: (*a*) S-Zolzap Creek, (*b*) S-Quinsam River, (*c*) S-Puntledge River, (*d*) S-Bulkley River Up, and (*e*) S-Babine River. Data from Zolzap Creek (row *a*) are for wild fish; all other data are for hatchery stocks. Circles identify mean length at release and mean growth increments for multiple groups of fish marked with unique tag codes and from different cohorts. Trend lines are loess smooths. Smooth curves were fitted only when there were at least 10 data points in a panel and the range of smolt lengths was at least 10 mm.

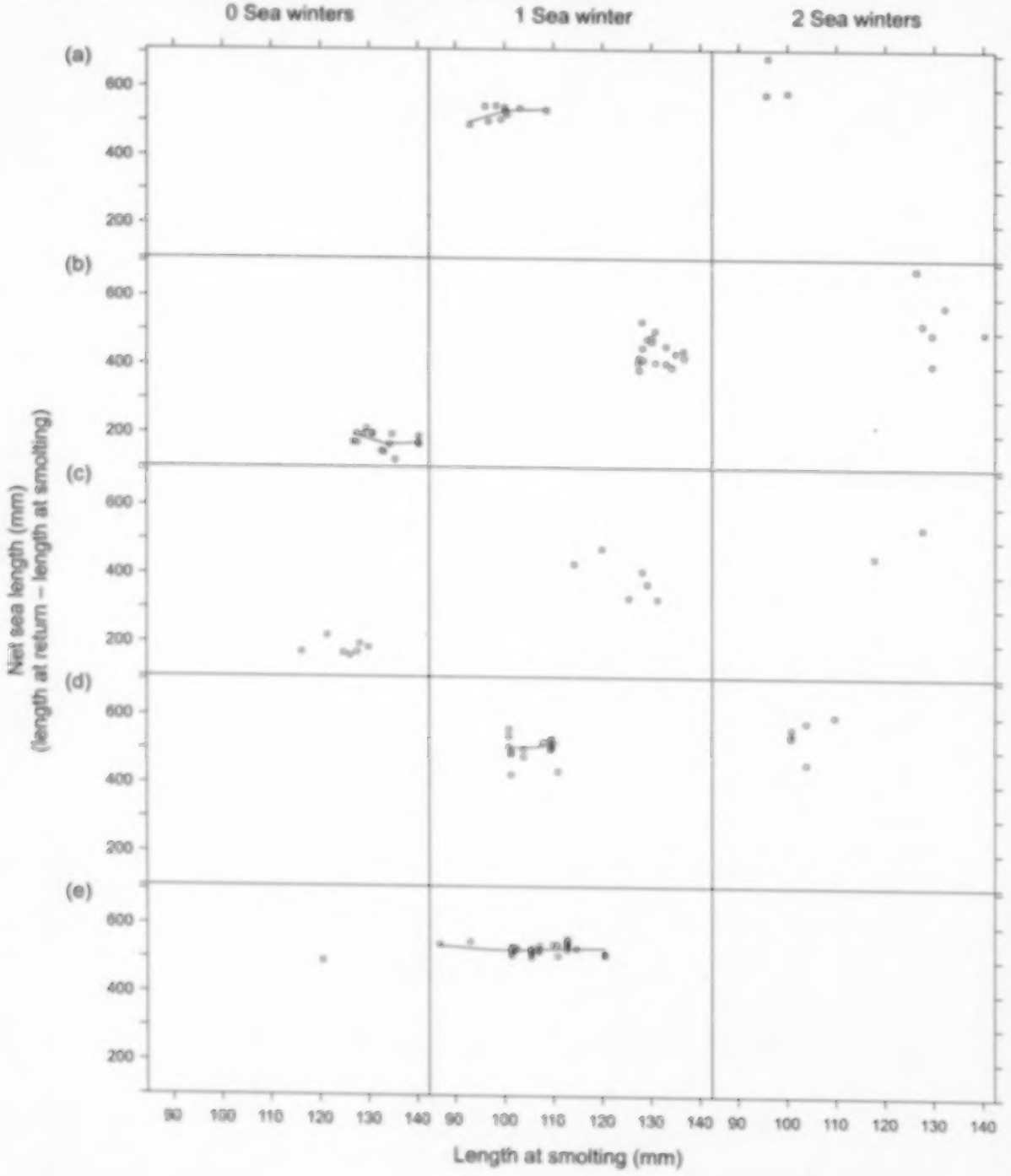

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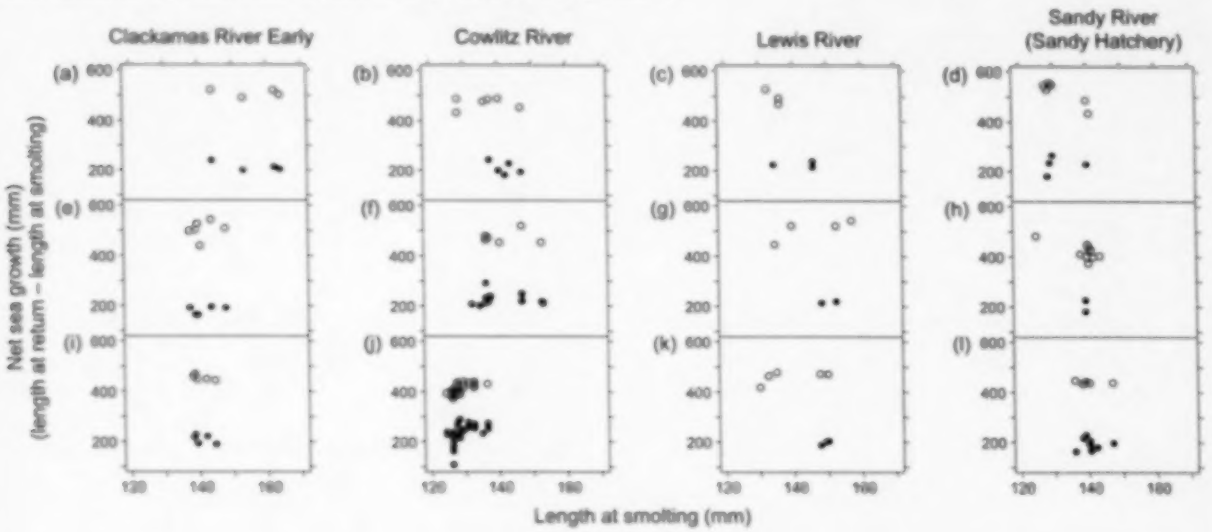
Fig. 6. Cohort-specific net growth of coho salmon (*Oncorhynchus kisutch*) released as age 1+ smolts from four hatchery stocks in the Columbia River Basin. The data are a subset of those presented in Figs. 3 and 4. Columns are identified by stock location names recorded in the Coded Wire Tag (CWT) database. Panels are identified by the year in which smolts were released: (*a*) 1996, (*b*) 1992, (*c*) 2000, (*d*) 1994, (*e*) 1993, (*f*) 1986, (*g*) 1998, (*h*) 1992, (*i*) 1991, (*j*) 1982, (*k*) 1996, and (*l*) 1991. These years were arbitrarily selected to represent the range of responses seen in the CWT data. Solid circles are estimated growth increments for fish that spent zero winters at sea, and open circles are estimated growth increments for fish that spent one winter at sea. Each circle identifies the mean size at smolting and mean growth increment for a group of fish that shared a common tag code recorded in the CWT database (note, however, that all tag codes within a panel identify fish from a single cohort).



ships between pre- and post-smolt growth performance of coho salmon. Relationships between smolt length and net growth at sea were mostly absent for 0- and 1-sea-winter coho from stocks in Oregon (Fig. 3). For the five coho stocks from Washington, the relationships for 0-sea-winter fish were slightly negative or absent (Fig. 4), and the relationships for 1-sea-winter fish were mainly absent or positive (Fig. 4). The data from British Columbia were sparse and difficult to interpret, but relationships between smolt length and net growth at sea were predominately absent for both 0-sea-winter and 1-sea-winter coho (Fig. 5). Data for 2-sea-winter coho from all 15 stocks represented by the CWT data were sparse, and trends ranged from negative to positive (Figs. 3–5).

When we controlled for annual variability in oceanographic conditions, additional variation in the relationship between smolt length and growth performance at sea was revealed (Fig. 6). For example, 1-sea-winter coho from the Lewis River showed the possibility of a negative relationship in 1 year and positive relationships in 2 subsequent years (Figs. 6*c*, 6*g*, and 6*k*). Similarly, for fish from the Sandy River, a negative relationship was suggested for two of the years, and no trend was suggested in a third year (Figs. 6*d*, 6*h*, 6*l*). Overall, the cohort-specific average relationships between smolt length and growth performance at sea varied from negative to positive, as with the CWT data that were combined across cohorts and years.

Relationships between pre- and post-smolt growth performance recorded in the literature were not as varied as those from the CWT data. Negative relationships between smolt length and net growth at sea were primary for 0-sea-winter coho (Fig. 7). For 1-sea-winter and 2-sea-winter fish from hatchery and wild stocks, relationships were absent or negative (Fig. 7).

We compared patterns observed in the CWT and literature data with predictions from our growth model. In our model, negative relationships between freshwater and salt-water growth performance corresponded to cases where $0 \leq \psi \leq 0.25$, while relationships were absent when $0.25 \leq \psi \leq 0.5$. These ranges of ψ appeared to be the most descriptive for 0-sea-winter coho (Figs. 2–5), suggesting that resources were well to moderately mixed at sea and were not defensible by dominant or aggressive coho smolts. For 1-sea-winter and 2-sea-winter coho, the relationships ranged from positive to negative, but the majority showed no clear relationship (Figs. 3–5). In comparing these observations with our predictions, a parameterization of $0.25 \leq \psi \leq 0.75$ appeared most appropriate. This suggested that as the coho grew and spent more time at sea, they gained increased access to food resources as dominant or aggressive behaviors became more effective.

Discussion

We offer a theory that unifies the conflicting relationships (see the references that were cited in the Introduction) observed between freshwater and salt-water growth performance by salmonids. This unification is achieved by considering growth in terms of the behavior–environment interaction. Effective dominance behaviors combined with re-

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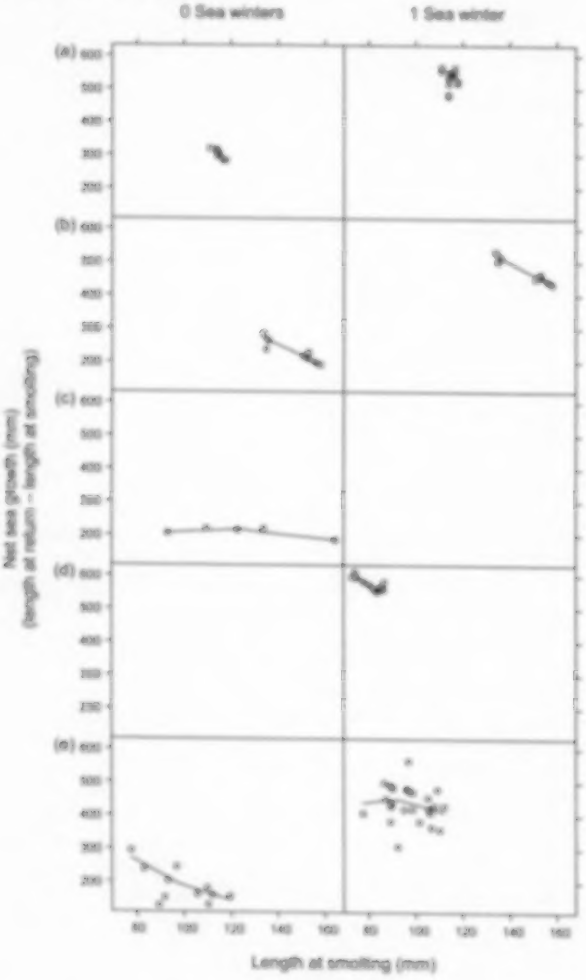
Fig. 7. Average net growth of coho salmon (*Oncorhynchus kisutch*) reported in the literature. Rows are identified by author: (*a*) Shapovalov and Taft (1954), (*b*) Mathews and Ishida (1989) (note that the data for 0 sea winters are back-calculations of length at the first ocean annulus on scales), (*c*) Hager and Noble (1976), (*d*) Holtby and Healey (1986), and (*e*) University of Washington Hatchery. Fish represented by data in row (*e*) were released as age 0+ smolts; all other fish were released as age 1+ smolts. Circles are estimated growth increments, and trend lines are loess smooths. Smooth curves were fitted only when there were at least five data points in a panel and the range of smolt lengths was at least 10 mm.



source distributions that are clumped at appropriate scales lead to positive relationships between freshwater and salt-water growth. On the other hand, ineffective dominance behaviors combined with relatively well-mixed resources lead to negative relationships between freshwater and salt-water growth. Infinitely many behavior–environment interactions are possible, and the signs and strengths of relationships between freshwater and salt-water growth performance will vary in response to these interactions.

We used coho salmon as a case study, and laboratory observations of this species seem to confirm the influence of the behavior–environment interaction. Paszkowski and Olla (1985) found both that postsmolt coho remained territorial and aggressive for months after the smolt transformation and that the most aggressive fish acquired the most food. Importantly, however, Paszkowski and Olla (1985) presented food to captive fishes at a single source, thus providing a consistent and defensible resource that might not be found in the ocean. In another laboratory experiment on coho parr, Ryder and Olla (1996) presented food in both localized and dispersed manners. Aggressive behaviors did not differ between the two feeding regimes, but all individuals had equal access to food resources when food was dispersed over the tank while only the most aggressive fish acquired food under the localized treatment. Together, these two studies (and many of the studies mentioned in the Introduction) reiterate the necessity for caution in making inferences from the growth of captive fishes. Variation in the method of feeding may influence the relationship between pre- and post-smolt growth performance. More importantly, these studies suggest that while coho may remain aggressive after the smolt transformation, aggressive individuals will not necessarily acquire more resources — resource acquisition also depends on environmental conditions.

Ineffective aggression (i.e., defending territories that do not offer competitive advantages) may have detrimental consequences for growth at sea. The largest coho smolts are probably the most territorial in fresh water (Martel 1996), and Vøllestad and Quinn (2003) found that the growth rates of territorial coho parr actually decreased when food was presented in a dispersed manner and made equally available to all individuals. Aggressive, territorial individuals have higher metabolic demands than their nonterritorial counterparts (Puckett and Dill 1985; Vøllestad and Quinn 2003), and if aggression does not increase resource acquisition, high metabolic demand may ultimately slow growth at sea (Vøllestad and Quinn 2003). The CWT and literature data presented here suggest that when coho spend only one growing season at sea, the same territorial behaviors that increase growth rates in fresh water have either no effect on or a potentially detrimental effect on growth rates in salt water.

For coho that spend more than one growing season at sea, the relationship between freshwater and salt-water growth performance is less clear. In most instances, we did not find convincing average relationships between smolt length and net growth of 1-sea-winter and 2-sea-winter fish. This suggests that dominance behaviors can be ineffective for acquiring resources in the second and third growing seasons, opposite of what appears to be likely in the first growing season. We did, however, find some positive relationships for coho that mature late, suggesting that the effectiveness of aggression and dominance can increase as coho spend more time at sea. Our model does not currently allow an individual's foraging range to increase as that individual grows. One can envision that as the ratio of an individual's foraging area to the area over which resources are distributed increases, resources may be more readily acquired and aggressive behaviors may be more effective. It may be more realistic to parameterize E_{sw} so that ψ is a function of length

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or age that reflects possible ontogenetic shifts in the effectiveness of aggressive behavior.

Clues about alternative parameterizations of ψ might be obtained from scales and otoliths of spawners. For example, length- or age-specific estimates of ψ might be developed from back-calculated lengths at smolting, at the end of the first growing season, and at the end of the second growing season. Additionally, scales obtained from individuals in the same stock but different cohorts could provide information on the degrees to which environmental conditions affect ψ. Ultimately, it may be possible to relate growth performance to indices of oceanographic condition and predict how growth performance changes in response to environmental forcing. Such studies were, in fact, motivations for us to develop the growth model described here.

We have noted age-specific differences in the relationships between growth in fresh water and growth in salt water, but it is also striking that we observed substantial variation in these relationships across stocks and geographic regions. The CWT data presented here suggest that the different migratory paths and ocean conditions experienced by different stocks can affect the relationships between pre- and post-smolt growth performance. This suggestion must, however, be tempered by acknowledging that the stock-specific differences in growth performance noted here may be related to differential effects of hatchery practice. Nevertheless, over the geographic range of coho salmon, we do not expect a single relationship between freshwater and salt-water growth performance.

Negative relationships between freshwater and salt-water growth performance by salmonids have interesting implications for reproductive strategy. Theoretical studies of alternative reproductive tactics within a single sex suggest that for some measures of individual condition, there is a switch point at which an individual in condition greater than the switch point should choose an alternative reproductive strategy (Charnov 1993; Gross 1996). For coho salmon, the proposed measure of condition is juvenile body size (Charnov 1993) or smolt length. At a body size greater than the switch point, individuals are predicted to mature early. However, previously published studies do not provide the proximate mechanisms linking large smolt size and early maturation. In coho salmon, and possibly salmonids in general, that mechanism appears to be the habitat differences associated with anadromy. Migrating from fresh water to salt water can have profound effects on growth performance because the behavior–environment interaction is abruptly altered. We intend to use our growth model as a foundation for developing fitness functions that predict ages at maturity conditioned on smolt size.

It is important to identify some of the caveats related to our work. In modeling freshwater growth, we set $\psi = 1$, making the assumption that the more dominant individuals will always be larger smolts. Some studies of Atlantic salmon indicate, however, that individuals with higher dominance status do not always display higher growth rates (Martin-Smith and Armstrong 2002; Harwood et al. 2003). Martin-Smith and Armstrong (2002) found no relationship between growth, measured as specific growth rate and aggressive behavior in Atlantic salmon. They studied fish in a seminatural stream system supplied with natural food sources, and their results suggest that it is possible that $\psi < 1$ in some freshwater environments. We did not consider $\psi < 1$ in our model, as the overwhelming evidence for both hatchery and wild coho indicates that $\psi = 1$ (Puckett and Dill 1985; Nielsen 1992; Martel 1996). Nevertheless, future applications of our model, particularly to other salmonids, may need to consider other values of ψ in fresh water.

We also assumed that k remains the same in both habitats, and this assumption may need further evaluation. As noted in the Methods section, k is closely related to metabolic rate and activity (Beverton and Holt 1959). Morgan and Iwama (1998) found no difference between the oxygen consumption rates of coho salmon in fresh water and salt water, but temperature was held constant in all treatments. There is a positive relationship between environmental temperature and k (Beverton and Holt 1959), and it is possible that k declines upon out-migration to cooler temperatures in the ocean. We considered a formulation in which k was habitat-specific:

$$k_{SW} = k_{FW} - \kappa$$

where κ is the average decline in k from fresh water to salt water. The qualitative predictions of this formulation did not change from those described previously. It is also possible that rankings of k may switch upon the out-migration (i.e., the smolts with the largest k switch to having the smallest k), as, from a physiological standpoint, what works well in fresh water may not work well in salt water (Thorpe 1987; Einum et al. 2002). This seems unlikely from the data presented here and from the studies cited in the Introduction, as one would expect negative relationships between freshwater and salt-water growth rates to be predominant.

We have presented a growth model that describes growth stanzas typical of salmonid life histories. This growth model can accommodate the life history of any salmonid (and possibly any diadromous fish) and is flexible enough to allow for all possible relationships between freshwater and salt-water growth performance. Appropriate parameterizations of anabolism can be determined both by considering how behavior and environmental conditions interact to affect resource acquisition and by making appropriate observations (e.g., analyses of mark–recapture data, otoliths, and scales). We presented a case study for coho salmon and suggest that during the first salt-water growing season, aggressive behaviors interact with environmental conditions in a way that does not facilitate increased resource acquisition by large smolts. During subsequent growing seasons, aggressive behaviors may or may not interact with environmental conditions to increase resource acquisition. Ultimately, the relationship between freshwater and salt-water growth performance will vary by stock and geographic region.

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Spatial and temporal variation in the influence of density dependence on growth of stream-living brown trout (*Salmo trutta*)

Javier Lobón-Cerviá

Abstract: The objective of this study was to investigate the extent to which, and the conditions under which, density operated on growth in stream-living brown trout (*Salmo trutta*). Observational data of 14 cohorts at four sites of Rio Chaballos (northwestern Spain) were examined. Consistent relationships between cohort-specific mass versus cohort-specific density and between year-to-year variations in brown trout mass at the end of five successive life stages versus mean densities corroborated one another and provided compelling evidence for the occurrence of density-dependent growth. However, density-dependent patterns varied in nature among sites to the extent that they were site-specific. A further comparison among 12 data sets revealed a smooth negative power trajectory between juvenile mass versus density. This plot suggested that detection of density-dependent growth might be facilitated in low density – high growth populations located at the steep wing relative to high density – slow growth populations. Current results emphasized the importance of density as a factor determining size-at-age and supported its operation as epiphenomena capable to obscure the effects of temperature on growth. The operation of density-dependent growth on numerical regulation of the population is further discussed.

Résumé : L'étude de l'importance du rôle de la densité et des conditions dans lesquelles la densité agit sur la croissance de truites brunes (*Salmo trutta*) vivant en cours d'eau constituent l'objectif de ce travail. Des observations portant sur 14 cohortes à quatre sites du Rio Chaballos (nord-ouest de l'Espagne) ont été analysées. Il y a des relations cohérentes entre la masse et la densité de chacune des cohortes et entre les variations inter-annuelles de la masse de la truite brune à la fin de cinq étapes successives du cycle biologique et les densités moyennes; ces relations se corroborent mutuellement et fournissent des preuves convaincantes que la croissance est dépendante de la densité. Cependant, la nature des patrons de dépendance de la densité varient d'un site à l'autre au point où ils sont spécifiques à chaque site. Une comparaison additionnelle de 12 séries de données indique qu'il existe une relation régulière de puissance négative entre la masse et la densité chez les jeunes truites. Ce graphique indique que la dépendance de la croissance de la densité peut être plus facile à déceler dans les populations de faible densité et à forte croissance situées dans la partie à forte pente de la courbe, par rapport aux populations de forte densité à croissance lente. Ces résultats mettent en lumière l'importance de la densité comme facteur de détermination de la taille en fonction de l'âge et ils indiquent que la densité agit comme épiphénomène capable de masquer les effets de la température sur la croissance. L'action de la croissance dépendante de la densité sur le contrôle numérique de la population fait l'objet d'une discussion plus poussée.

[Traduit par la Rédaction]

Introduction

In fishes, individual growth is a fundamental element upon which a variety of life history traits depend (Wootton 1998). Among the numerous factors that may influence size-at-age, density-dependent growth concerns reduced individual feeding rates with increased abundance of population members (Heath 1992). The effect of density on growth typically results in variations in age at maturity (Hutchings and Jones 1998), fecundity and recruitment (Cowan et al. 2000), and density-dependent mortality (Rose et al. 2001). Therefore, a potential exists for density-dependent growth to be a regulatory mechanism of population numbers (Lorenzen and Enberg 2001).

Stream-living salmonids have been the focus of intensive research, especially brown trout (*Salmo trutta*). Several decades of effort (Backiel and Le Cren 1967) to identify the factors determining growth variations within and among populations (Klemetsen et al. 2003) have included long-term assessments and experimental approaches. While support for the occurrence of density-dependent growth has been gleaned from experimentation in artificial channels (Jenkins et al. 1999; Keeley 2001) or manipulation of densities of stream populations (Weiss and Schmitz 1999; Nordwall et al. 2001; Bohlin et al. 2002), observational studies have seldom identified density-dependent growth in the youngest juveniles (Le Cren 1973; Crisp 1993; Jenkins et al. 1999).

Difficulties in detecting density-dependent growth in stream-living brown trout may stem from the variety of factors affecting growth. Water temperature, food availability,

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density, and size-selective mortality are the most common explanations for variations in size-at-age (Elliott 1994). Growth rates have been shown to be continuously and nonlinearly related to water temperature (Elliott 1975*a*; Jensen et al. 2000; Ojanguren et al. 2001). Where individuals feed close to or at satiation, growth rates are determined by water temperature albeit optimum temperatures may vary under variable food ratios (Elliott 1975*b*; Forseth and Jonsson 1994) to the extent that the expected direction of the temperature effects may depend on interaction between temperature and food ratios (Elliott 1975*a*, 1975*b*). Several authors, however, have suggested that variations in size-at-age across populations are determined by stream temperatures (Edwards et al. 1979; Elliott et al. 1995; Jenssen et al. 2000). In turn, increased density might constrain individual feeding rates through reduced prey and habitat availability (Klemetsen et al. 2003) or through decreased territory size (Grant 1997) or increased defense costs (Hixon 1980), resulting in suppressed growth (Jenkins et al. 1999). Size-selective mortality acting on the smaller or larger individuals might enhance variations in size-at-age (Sinclair et al. 2002).

Moreover, egg size (Lobón-Cerviá 2000), resources availability (Gibson and Galbraith 1975), current velocity (Mason 1976), and exceptional climatic events such as floods (Waters 1999) and droughts (Elliott et al. 1997) have also been reported to induce variations in size-at-age. And, though resident brown trout are predominantly sedentary (Hesthagen 1990; Bridcut and Giller 1993), mobile individuals may interact with habitat heterogeneity (Rodriguez 2002) to obscure the effects of density on growth.

In such scenarios, disentangling the effects of the factors above to isolate the operation of density requires at least (*i*) examination of long-term, simultaneous quantifications of temperature, growth, and density that permit the isolation of single effects of density from temporal variations and from the effects of temperature and mortality and (*ii*) replicate habitats (Ray and Hasting 1997) to identify the ranges upon which density attains the thresholds needed to be functionally operative (e.g., where food, space, or other resources do not constrain its operation; Mortensen et al. 1988; Jenssen 1990).

This study investigated the extent to which, and the conditions under which, density might operate on growth across the habitat complexity that is typical of Cantabrian streams (northwestern Spain). This study focused on the brown trout population of Rio Chaballos where previous studies revealed stationary behavior, negligible mortality during 50%–60% of life span, and substantial variations in growth and density across spatio-temporal scales (Lobón-Cerviá 2000, 2003). This situation of low mortality during a prolonged time interval in which individuals experience the same temperatures (Lobón-Cerviá and Rincón 1998) and extreme differences in density can be expected to show the most pronounced effects on growth (Backiel and Le Cren 1967) and makes this population an exceptional candidate for elucidating the role of density on growth in a purely observational study.

The main objective of this study was to answer the following questions. (*i*) Are spatio-temporal variations in growth related to water temperature? (*ii*) If not, are those variations in growth related to density? (*iii*) If density is a major factor, what is the shape of those relationships across scales of space and time? (*iv*) What is the importance of intracohort density relative to accompanying cohorts? Finally, (*v*) what proportion of growth variation is accounted for by density relative to temperature or other factors across scales of space and time?

Recently, Jenkins et al. (1999) have argued that because growth-density relationships describe negative power trajectories, density-dependent growth might be undetected in high-density populations. As a secondary objective of this study, I revisited the hypothesis of Jenkins et al. (1999) to place growth-density relationships for Rio Chaballos within the ranges of growth and density reported for stream-living brown trout populations. First, I explored whether the patterns elucidated for Rio Chaballos were corroborated by a similar data set collected on a nearby population showing comparable ranges of growth and density. Second, these two populations were incorporated into a broad comparison among populations reported in the literature that includes the life history modes exhibited by the species and the extremes of growth and density observed in stream populations within the distributional range.

Materials and methods

Data collection

This study was done on Rio Chaballos (Rio Esva drainage, Asturias, northwestern Spain). Environmental characteristics of this stream and the study sites have been described elsewhere (Lobón-Cerviá and Rincón 1998; Rincón and Lobón-Cerviá 2002; Lobón-Cerviá 2003); therefore, only details relevant for this study are included.

The data set was collected during a long-term monitoring program that continues from 1986. Four stream sites (S1 to S4) of similar length (60–80 m) and width (2–6 m), located about 1 km apart, were selected to include the habitat heterogeneity apparent along the 5-km-long stream. In this stony bottom stream, cobble dominated the substrate composition (30%–60%) of the four study sites. Sites S1, S2, and S3 were surrounded by meadows with little bank vegetation and were similar in area (240, 253, and 218 m^2) and depth (18.3, 18.4, and 16.5 cm). In contrast, site S4 was fully covered by bank vegetation (97% of the surface area) and showed greater width (5 m), area (370 m^2), and depth (0.25 m) because of the occurrence of a large (35 m^2) and deep (≈1 m) pool by the middle of the site. Daily water temperatures were recorded just above and below the study sites (Lobón-Cerviá and Rincón 1998).

Brown trout size and density were tracked for the 14 cohorts hatched in the years 1986 to 1999 (1988–1999 at site S2). Census data were obtained every second month (January, March, May, July, September, and November). For all samples, the sites were blocked with nets to apply the three-removal method with electrofishing techniques (Carle and Strub 1978; Lobón-Cerviá 2003). All individuals captured were measured (fork length, mm) and assigned to age classes easily detectable from the length–frequency distributions. During the early years of study, the age of individuals was validated by scale readings. In later years, scales were only used to confirm doubtful assignments of larger (older) individuals. Length–frequency distributions for each sampling site and date were transformed into mass distributions

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(Nielsen and Schoch 1980) based on length-to-weight keys established from samples collected during the years 1986–1995 (Lobón-Cerviá and Rincón 1998).

The number of individuals for each site and date was estimated separately for age-0, age-1, and older individuals. Each estimate was tested for failure condition and goodness of fit (Otis et al. 1978; Seber 1982). This analysis revealed a highly efficient capture performance across seasons and sites with a 90% (range 81%–98%) average capturability for ≥ age-1 individuals and 75% (range 66%–82%) for age-0 individuals (Lobón-Cerviá 2003). A second data set collected by applying the same methods and techniques was used for comparative purposes (J. Lobón-Cerviá, unpublished data). This data set encompasses mass and density of juveniles in May and September over 11 successive cohorts (1990–2001) at three sites (V1, V2, and V3) of Rio La Viella, which flows near Rio Chaballos within Rio Esva drainage.

Brown trout population

In this spatially continuous population, all individuals experienced the same water temperature (Lobón-Cerviá and Rincón 1998). Nevertheless, growth, density, and life span differed among sites. Life span ranged from 30–32 months at site S1 to 42–46 months at site S4. The population was therefore composed of age-0 to age-3 individuals, with the latter primarily at site S4. Among-site differences in age structure persisted over the years, consistent with a stationary behavior revealed by extensive marking procedures (Lobón-Cerviá 2000, 2003).

Emergence was assumed to occur simultaneously at all sites on March 15 (i.e., population birth date). In previous studies, Lobón-Cerviá (2004) and Lobón-Cerviá and Rincón (2004) documented that the survival rates of recruits (i.e., the abundance of youngest juveniles that incorporated to the population as result of annual reproduction) was determined by stream discharge in March (at the time of or just after emergence) but differed among sites in relation to stream channel structure. Once recruits incorporated to the population, survivor's abundance over time described two-phase trajectories split by a break point. A first phase lasting for 500 days after emergence (average among cohorts, at site S1), 490 days (at site S2), 530 days (at site S3), and 650 days (at site S4) was followed by a second phase characterized by steeper declines or severe mortalities. Brown trout size at the break point when mortality switched from negligible to severe was remarkably similar among sites (15 cm, 40 g) despite that this size was attained about 1 year later at site S4 relative to site S1 (Rincón and Lobón-Cerviá 2002; Lobón-Cerviá 2003). Gonadal development occurred from the first birth date onwards and all 21-month-old individuals >11 cm spawned at all sites and years (Lobón-Cerviá et al. 1997).

Data analysis

The occurrence of density-dependent growth was examined at two different levels. The first exploration focused on whether cohort strength had a negative influence on cohort growth. For this purpose, cohort-specific mass and cohort-specific density were measured by averaging mass (g) and density (individuals·m^{-2}) of each cohort and site from the first sample (May, 2-month-old individuals) up to 30-month-old individuals.

Secondly, to identify major life stages when density affected growth, brown trout mass and growth rate were obtained for five successive 4-month intervals. These time intervals corresponded to the following life stages: May–September (life stage 1, 60 to 180 days old), September–January (life stage 2, 180 to 300 days old), January–May (life stage 3, 300 to 420 days old), the second May–September (life stage 4, 420 to 540 days old), and the second September–January (life stage 5, 540 to 660 days old). Thus, these life stages included growth and density from the youngest juveniles (i.e., life stage 1) and gonad development (i.e., life stages 3 and 4) to first spawning (i.e., life stage 5). Across life stages, mortality occurred during life stage 5 at site S4 and during life stages 4 and 5 at sites S1, S2, and S3.

Differences in growth and mortality during a time interval may obscure actual growth–density or growth–temperature relationships. Therefore, the effects of density on mass were explored by inspecting the trajectories described by brown trout mass at the end of each 4-month life stage over the mean density during that life stage. These mean densities were calculated according to D (individuals·m^{-2}) = $(D_2 + D_1)/2$, where D_1 and D_2 are densities at the beginning and end, respectively, of each life stage. Similarly, comparisons were made between daily instantaneous growth rates (G) for each life stage and mean stream temperatures (T, °C) during that life stage. Growth rates were calculated for each life stage and site according to $G = 100\log(W_2 / W_1)/t$, where W_1 and W_2 are the mean weights at the beginning and end, respectively, of each life stage and t is the number of days between samples (120 days, range 100–135 days).

Because the effect of density on growth may occur among members of the same cohort or among members of different cohorts (i.e., intra- or inter-cohort interactions, respectively), the effects of density on brown trout mass and growth rates were explored for intracohort density (the life-stage-specific density of the current cohort) and intercohort density (the life-stage-specific density of the accompanying cohorts) as predictor variables versus life-stage-specific mass or growth rate as response variable.

Year-to-year variations in juvenile mass at the end of the first summer growth (September) versus mean density during that summer (life stage 1, May–September) were compared between Rios Chaballos and La Viella. These two populations were further incorporated into a broad comparison including 12 data sets either unpublished or collected from the literature: Rio Chaballos (four study sites; this study), Rio La Viella (three study sites; J. Lobón-Cerviá, unpublished data), Convict Creek (three study sites, California; Jenkins et al. 1999), Black Brows Beck (one study site, northern England; Elliott 1994), and Shelligan Burn (one study site, Scotland; Egglishaw and Shackley 1977). This comparison included the maximum range of growth and densities reported for stream-living brown trout populations and the reproductive modes exhibited by the species: resident (this study), anadromous (Elliott 1994), combined resident + anadromous (Egglishaw and Shackley 1977), and introduced resident (Jenkins et al. 1999) populations.

The percent habitat saturation index (PHS; Grant and Kramer 1990) was used as a relative indicator of the levels

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to which the study sites may become overcrowded. Grant et al. (1998) provided an equation to quantify habitat occupation for single or combined cohorts: PHS = 100ΣD·TS, where D is density (individuals·m^{-2}) and TS is the territory size (m^2). The latter was obtained from the negative power function: logTS = 2.61·log length (cm) – 2.83 (Grant et al. 1998). PHS values equal 100% when the population is at the carrying capacity and fish show a total occupancy of the habitat. Because of size-dependent habitat availability (Rincón and Lobón-Cerviá 2002), only parts of the stream are suitable for fish of a given size. Grant and Kramer (1990) suggested that density-dependent responses should be expected for PHS values > 27%.

Numerous studies (Backiel and Le Cren 1967; Crisp 1993; Jenkins et al. 1999) have shown that the shape of growth (G) – density (D) relationships is described by a negative power function i.e., $G = aD^b$. The log-transformed linear version ($\log_{10}G = \log_{10}a + b\cdot\log_{10}D$) was used to analyze growth–density relationships. Analysis of covariance (ANCOVA) was used to compare linear regressions. Repeated-measures analysis of the variance (RM-ANOVA; von Ende 2001) was used to explore the effects of the site (between-subject) and life stage (within-subject) on successive measures of brown trout mass (W), growth rate (G), and density (D) over time.

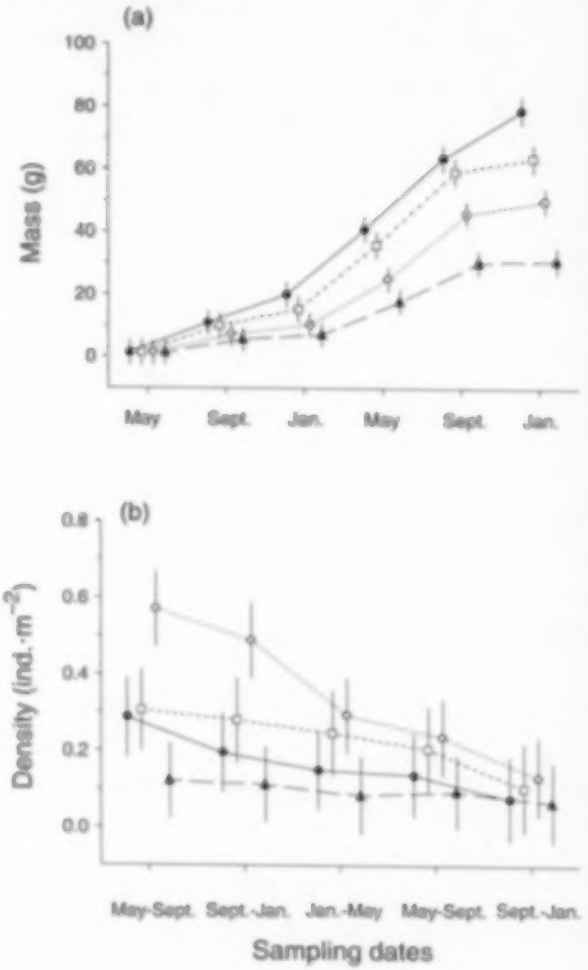
Results

Spatio-temporal variations in growth and density

The mass attained by the youngest juveniles (May, 2-month-old individuals, initial mass) showed highly significant among-cohort differences ($F_{[13]} = 3.85$, $p = 0.0004$). Among-site differences across years verged on significance ($F_{[3]} = 2.5$, $p = 0.07$, mean mass = 1.2, 1.2, 1.1, and 1.4 g for sites S1 to S4, respectively). However, after the first summer growth, the mass attained by brown trout individuals differed markedly among sites (Fig. 1*a*). At sites S1 and S2, 6-month-old juveniles attained double the mass of their counterparts at site S4 (10.5 and 9.8 g versus 5.4 g), with individuals at S3 showing intermediate values (7.2 g). Despite substantial differences among cohorts, the among-site differences in mass continued to increase over life stages (Fig. 1*a*) to an extent that RM-ANOVA revealed strong significant effects (at least $p \leq 0.01$) of the site and cohort on mass and growth rate across life stages (Table 1).

The abundance of the youngest juveniles (i.e., 2-month-old individuals) showed ≈100-fold variation (range 0.02–1.9 individuals·m^{-2}) among cohorts and among sites. The abundance of older individuals showed similar magnitudes of variation across life stages, cohorts, and sites (Fig. 1*b*). Repeated-measures ANOVA revealed significant effects (at least $p \leq 0.001$) of the site and cohort on density across life stages (Table 1). Thus, while the mass of the youngest juveniles upon which growth was examined was relatively similar among sites, a strong effect of the site and cohort on growth and abundance was expressed in significantly greater growth at sites S1 and S2, greater density at site S3, and lower growth and lower density at site S4 (Fig. 1).

Fig. 1. (*a*) Mass-at-age (g, ±1 standard error, SE) averaged across cohorts in May, September, January, and the second May, September, and January, and (*b*) mean densities (individuals·m^{-2}, ±1 SE) averaged across cohorts for the five successive 4-month life stages (May–Sept., Sept.–Jan., and Jan.–May and the second May–Sept. and Sept.–Jan.) of brown trout (*Salmo trutta*) individuals examined at four study sites S1 (●), S2 (□), S3 (◇), and S4 (▲) of Río Chaballos.



Habitat occupancy

PHS values for single cohorts indicated that habitat occupation by life-stage-1 individuals was greater at all sites in years of greater recruitment ($R^2 = 0.85$, $p < 0.001$) and decreased exponentially with individual mass for site S1 ($R^2 = 0.40$, $p = 0.01$) and for pooled sites S1–S3 ($R^2 = 0.30$, $p < 0.001$), but this relationship was not significant for site S4 ($R^2 = 0.10$, $p = 0.24$). As indicated by PHS values, habitat occupancy increased over life stages (ANOVA, $F = 1.9$, $p = 0.0001$) to a maximum at life stage 4 and a slight decrease at life stage 5. However, the amount of habitat occupied by the current cohort differed among sites (ANOVA, $F = 30.0$, $p < 0.0001$). Thus, among-cohort and among-site variations in

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Table 1. F values and degrees of freedom ($F_{[df]}$, all significant in, at least, $p \leq 0.001$) from repeated-measures analysis of variance for the effects of the site and cohort (between-subject), and life stage (within-subject) and the corresponding interactions on trout mass (W), growth rate (G), and density (D) measured over successive life stages at the four study sites (S1 to S4) of Rio Chaballos.

	W	G	D
Site	$51.7_{[3,35]}$	$15.6_{[3,36]}$	$13.8_{[3,36]}$
Cohort	$2.5_{[13,35]}$	$2.9_{[13,36]}$	$5.0_{[13,36]}$
Life stage	$1123.5_{[5,175]}$	$846.3_{[4,144]}$	$39.2_{[4,144]}$
Life stage × site	$37.6_{[15,175]}$	$8.6_{[12,144]}$	$7.1_{[12,144]}$
Life stage × cohort	$2.0_{[65,175]}$	$2.8_{[52,144]}$	$2.4_{[52,144]}$

PHS values for life-stage-1 individuals ranged from 1.4% to 38.6% at site S1, from 4.1% to 43.9% at site S2, from 10.0% to 77.0% at site S3, and only from 1.4% to 8.3% at site S4. Maximum habitat occupancy at life stage 4 was 55.0% (S1), 105.1% (S2), 84.1% (S3), and only 22.5% (S4).

For all cohorts together, PHS values maximized at life stage 1 and decreased slightly (sites S1–S3) or remained similar (S4) over life stages. The ranges for PHS values for all cohorts together during life stage 1 across years ranged from 9.4% to 133.5% at site S1, from 25.6% to 221.1% at site S2, from 21.4% to 195.0% at site S3, and only from 7.7% to 41.4% at site S4. Slightly lower maximum values during life stage 4 were 93.8% (S1), 74.0% (S2), 123.6% (S3), and 49.1% (S4).

Growth rates versus temperature

Daily instantaneous growth rates (G) for the five life stages were plotted versus mean stream temperatures (T, °C). Linear regressions indicated negative trends between the growth rates of life-stage-1 individuals versus the mean temperatures during that period (range 13.2–19.0 °C). These negative relationships were highly significant (Table 2) at sites S2 ($R^2 = 0.68$, $p = 0.001$), S3 ($R^2 = 0.65$, $p = 0.0005$), and S4 ($R^2 = 0.45$, $p = 0.009$) but not at S1 ($R^2 = 0.14$, $p = 0.20$). Consistent with previous observations on growth rate – temperature relationships for these younger juveniles (Lobón-Cerviá and Rincón 1998), an ANCOVA for sites S2, S3, and S4 revealed significant differences among intercepts ($p < 0.001$) but not among slopes ($p = 0.64$). Thus, though growth rates differed among sites, year-to-year variation concurred with variation in temperature, except at site S1 where juveniles grew faster. No other significant growth rate – temperature relationships were detected for any other life stage or site.

Cohort-specific mass versus density

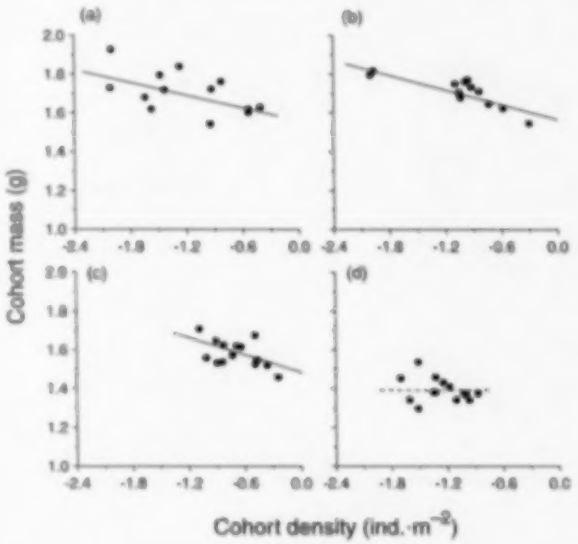
Log-transformed cohort-specific mass plotted against cohort-specific density revealed that stronger cohorts concurred with lower cohort masses (Fig. 2). Regression fitting detected statistically significant linear trends for sites S1 and S2 ($R^2 = 0.34$, $p = 0.03$, and $R^2 = 0.65$, $p = 0.001$, respectively), at the verge of significance for site S3 ($R^2 = 0.27$, $p = 0.058$,) and nonsignificant for S4 ($p = 0.18$). An ANCOVA for the regressions of sites S1 to S3 indicated different intercepts ($F_{[2,36]} = 7.59$, $p < 0.002$) but not slopes ($F_{[2,34]} = 0.71$, $p > 0.5$).

Table 2. Regression coefficients for the instantaneous growth rates of life-stage-1 individuals versus mean stream temperatures at the four study sites (S1 to S4) of Rio Chaballos.

	N	a	b	R^2	p
S1	14	2.638	–0.046	0.14	0.20 (NS)
S2	12	3.785	–0.133	0.48	0.01
S3	14	3.324	–0.112	0.65	<0.001
S4	14	2.708	–0.096	0.45	0.009

Note: N, the number of data; a and b, the intersects and slopes, respectively; R^2, the variance explained; p, the significance level; NS, not significant.

Fig. 2. Negative linear trends between log-transformed cohort-specific mass (g) versus cohort-specific density (individuals·m^{-2}) for the 14 cohorts hatched in the years 1986–1999 at sites S1, S2, and S3 and the 12 cohorts hatched in the years 1988–1999 at site S2. (*a*) to (*d*) represent, respectively, the four study sites (S1 to S4) of Rio Chaballos. Continuous and broken lines indicate significant and nonsignificant linear regressions, respectively.



Life-stage-specific mass versus density

Year-to-year variations in mass attained at the end of each life stage versus the corresponding mean densities were examined separately for the five life stages and for single and pooled sites. Correlation analysis showed no statistically detectable relationships between mass versus intra- and intercohort densities for pooled sites.

Consistent relationships were detected when analyzing single sites (Fig. 3). Linear fits for the log-transformed mass versus intracohort density revealed statistical significance for all life stages at site S1 (at least $p \leq 0.001$), for life stages 2–5 at site S2 ($p \leq 0.002$), and for life stages 4–5 at site S3 ($p \leq 0.02$) but not at site S4 (Fig. 3; Table 3), where no significant relationship was apparent (at least $p \leq 0.50$). As well, linear fits indicated statistical significance for mass

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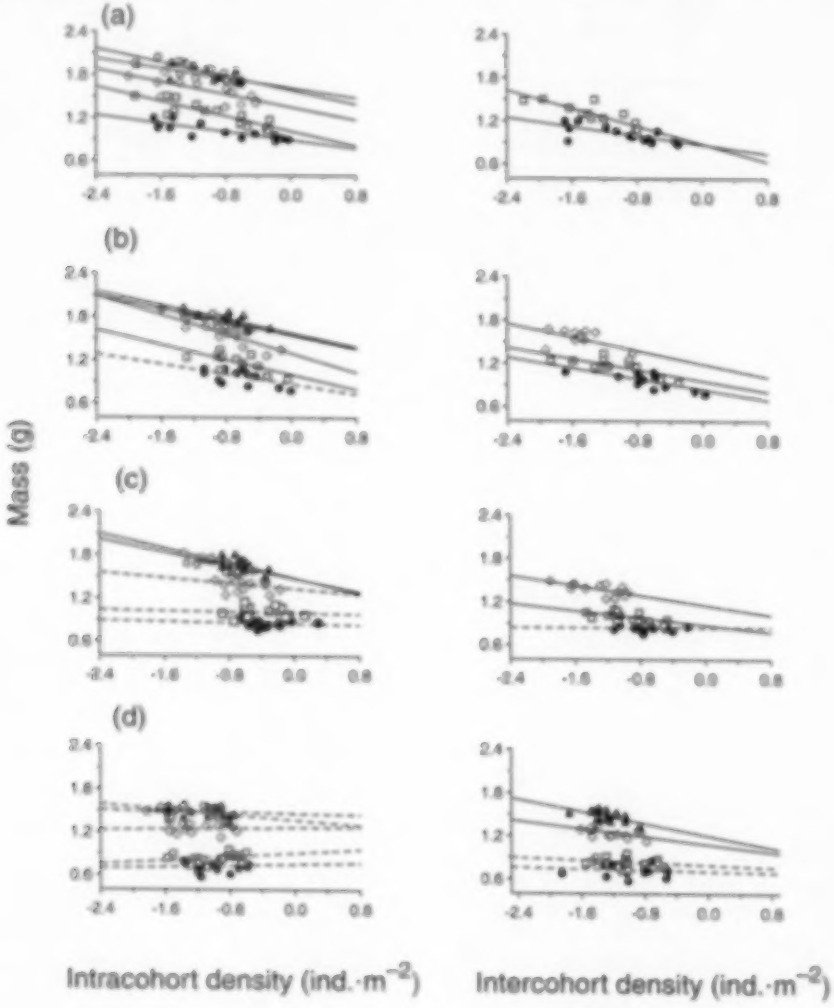
Fig. 3. Log-transformed life-stage-specific mass (g) at the end of five life stages versus intracohort and intercohort densities (individuals·m^{-2}). (*a*) to (*d*) represent, respectively, the four study sites of Rio Chaballos (i.e., S1 to S4). Symbols for successive life stages: life stage 1 (●), life stage 2 (□), life stage 3 (◇), life stage 4 (▲), and life stage 5 (○). Continuous and broken lines indicate significant and non-significant regressions, respectively.



versus intercohort density for the life stages available at sites S1 ($p \leq 0.006$) and S2 ($p \leq 0.01$), for life stages 2 and 3 at site S3 ($p \leq 0.02$), and for life stages 3 and 4 at site S4 ($p \leq 0.025$) (Fig. 3; Table 3).

Thus, intra- and inter-cohort densities were consistent predictors of the year-to-year variation in mass at sites S1 and S2 across life stages, with the only exception of intracohort density for life stage 1 at site S2. The predictive ability of intracohort density was negligible at S4, but not intercohort density for the older life stages. In addition, at site S3, intracohort density was a good predictor of brown trout mass for life stages 4 and 5, and intercohort density was a good predictor for life stages 2 and 3.

Analyses of covariance to compare linear regression relating life-stage-specific mass versus intra- and inter-cohort densities revealed no significant difference among slopes of intracohort ($F_{[10,117]} = 1.54$, $p > 0.5$) or intercohort ($F_{[8,94]} = 1.18$, $p > 0.05$) densities. Moreover, ANCOVA for pooled sets of regressions (20 regressions) revealed no significant differences among slopes ($F_{[19,212]} = 0.89$, $p > 0.6$), indicating similar overall effects of increased intra- and inter-cohort densities on life-stage-specific mass. Regression coefficients, significant levels, and variance explained for each life stage and site together with the ANCOVA results are summarized (Table 3).

Inspections of the patterns revealed for the four study sites (Fig. 3) indicated that the ranges of density upon which density operated on mass differed among sites. That is, at sites with similar density ranges, brown trout mass either varied around mean values or decreased with increased density. To provide further evidence of a site-specific operation of density, the second data set comprising data for juveniles during

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Table 3. Coefficients for the 20 linear regressions revealed significant (see Fig. 3) for the log-transformed trout mass (g) attained at the end of five successive life stages (1 to 5) versus (*i*) intracohort and (*ii*) intercohort densities (individuals·m^{-2}) at the four study sites (S1 to S4) of Rio Chaballos.

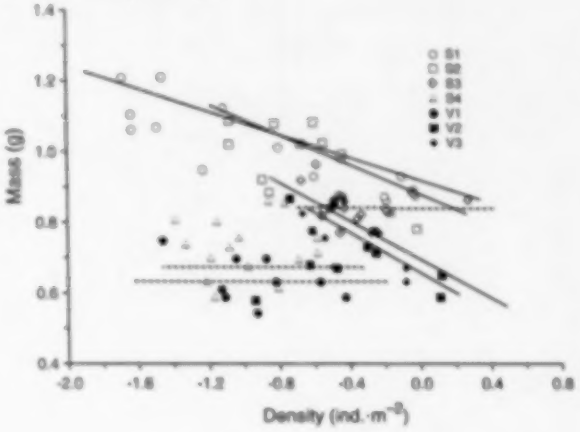
	Life stage	*N*	*a*	*b*	R^2
Intracohort densities					
S1: $F_{[4,54]} = 2.4$	1	14	0.896	–0.143	0.66
	2	14	1.023	–0.255	0.72
	3	12	1.357	–0.218	0.53
	4	13	1.622	–0.169	0.47
	5	11	1.592	–0.241	0.64
S2: $F_{[3,38]} = 0.39$	2	12	0.999	–0.262	0.59
	3	11	1.302	–0.322	0.61
	4	12	1.580	–0.241	0.61
	5	11	1.551	–0.228	0.76
S3: $F_{[1,24]} = 0.08$	4	14	1.480	–0.258	0.35
	5	14	1.475	–0.227	0.60
Pooled sites: $F_{[10,117]} = 1.54$					
Intercohort densities					
S1: $F_{[1,22]} = 4.40^{*}$	1	14	0.873	–0.155	0.48
	2	12	0.884	–0.307	0.58
S2: $F_{[2,28]} = 0.28$	1	12	0.871	–0.184	0.55
	2	11	0.936	–0.205	0.52
	3	11	1.196	–0.230	0.39
S3: $F_{[1,22]} = 0.29$	2	13	0.880	–0.122	0.31
	3	13	1.155	–0.168	0.42
S4: $F_{[1,24]} = 0.62$	3	14	1.093	–0.122	0.33
	4	14	1.213	–0.198	0.37
Pooled sites: $F_{[8,96]} = 1.18$					
Overall (a + b): $F_{[19,212]} = 0.89$					

Note: *N*, *a*, *b*, and R^2 are, respectively, the number of data, intersect, slope, and variance explained in the regressions fitted for each single life stage and site (all are significant to $p < 0.01$, at least). *F* values from analyses of covariance (ANCOVAs) indicated no significant differences in the slopes among life stages for each single site (i.e., S1 to S4, $F_{[df]}$) and among life stages for pooled sites (i.e., pooled sites, $F_{[df]}$) for either (*a*) intracohort or (*b*) intercohort densities. The only exception was life stage 1 versus life stage 2 at site S1 for intercohort density (*). An ANCOVA for the whole data set showed no significant differences among the slopes (i.e., overall, a + b).

the first summer at three sites of Rio La Viella (V1, V2, and V3) was examined and the results were combined with those of Rio Chaballos.

Linear fits to the trajectories described by log-transformed mass versus density for La Viella sites revealed significant negative correlations at sites V2 ($R^2 = 0.46$, $p = 0.04$) and V3 ($R^2 = 0.38$, $p = 0.04$) but not at site V1 ($R^2 = 0.12$, $p = 0.30$). A comparison among La Viella and Rio Chaballos sites was consistent with the hypothesis that density operated at a site scale within different ranges of density (Fig. 4). Brown trout masses at sites with similar density ranges either remained constant (S3) or decreased with increased density (V2 and V3). Moreover, brown trout mass did not vary where lower densities would have been expected to have pronounced effects on growth (S4 and V1) but did vary at sites S1 and S2 (Fig. 4). Consequently, there appears to be

Fig. 4. Comparative ranges of densities (individuals·m^{-2}) upon which juvenile mass (g) at the end of life stage 1 decreased with increased mean density at the four sites (S1 to S4) of Rio Chaballos and at three sites of Rio La Viella (V1 to V3). Continuous and broken lines indicate significant and nonsignificant regressions, respectively.



no threshold density common to all sites or streams at which density becomes functionally operative, i.e., its operation seems site-specific.

Life stage 1 mass versus density across populations

Year-to-year variations in juvenile mass at the end of the first summer versus mean densities during that time interval (April/May – August/September, except Convict Creek where only the final density was available) were compared among 12 data sets. This plot (Fig. 5) revealed that sites S1 and S2 of Rio Chaballos represent the maximum brown trout growth (maximum 14.5 g) and emphasized the occurrence of lower density and greater growth in resident (Rios Chaballos, La Viella, and Convict Creek) relative to anadromous (Black Brows Beck) and resident + anadromous (Shelligan Burn) populations. Apparently, populations with intermediate growth (>5 g) and densities (>2 individuals·m^{-2}) have not been documented for stream-living brown trout populations.

Despite dramatic spatio-temporal differences in growth and density among populations, juveniles' mass described a smooth negative power trajectory over density. The shape of this trajectory with substantially different slopes at high and at low densities is consistent with the hypothesis of Jenkins et al. (1999) that detection of density dependence would be facilitated in low density populations with potential for growth located at the steeper left-side wing of the curve, whereas such effects would be hardly detectable in high density populations located at the flat, right-hand side of the curve showing minor variation in growth.

Discussion

Density-dependent growth in Rio Chaballos brown trout

The observational data from this study collected over 14 successive cohorts across the environmental heterogeneity of

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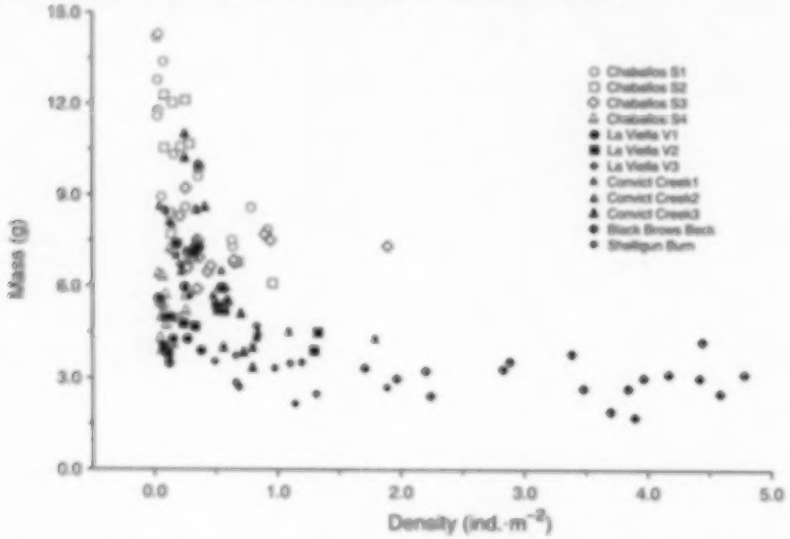
Fig. 5. Power negative trajectory described by juvenile mass (g) at the end of the first summer (September) versus mean summer density (individuals·m^{-2}) for 12 data sets: Rio Chaballos (sites S1 to S4; this study); La Viella (sites V1 to V3; Lobón-Cerviá, unpublished data.); Convict Creek1, Convict Creek2, and Convict Creek3 (California; Jenkins et al. 1999); Black Brows Beck (one site, northern England; Elliott 1994), and Shelligun Burn (one site, Scotland; Egglishaw and Shackley 1977).



Rio Chaballos showed substantial spatio-temporal variation in growth and density. Temporal variation of brown trout mass and growth in relation to temperature and density revealed growth rate – temperature relationships in the youngest juveniles, mass–density relationships across life stages and sites, and cohort-specific mass–density relationships at three out of four sites.

Negative relationships between cohort-specific mass versus density and between the year-to-year variation in the mass attained by brown trout individuals at the end of successive life stages and the corresponding mean densities corroborated one another and provided compelling evidence of density-dependent growth in Rio Chaballos brown trout. However, interactions between mass and density occurred at a site scale and varied in nature among sites to the extent that the overall patterns were site-specific.

Few observational studies have documented density-dependent growth in stream-living brown trout (Crisp 1993; Jenkins et al. 1999; Vollestad et al. 2002). The comparison among seven sites of two streams indicated that density operated at a site scale. Moreover, the negative power relationship between juveniles' mass versus density elucidated for 12 data sets suggested that the ranges of growth and density of the population under study might hinder detection of growth–density relationships. This was consistent with the fact that density-dependent growth reported for stream-living brown trout populations was detected where density ranges (0.1–2 individuals·m^{-2}; Crisp 1993; Jenkins et al. 1999; this study) were located on the steepest extreme of the curve, whereas growth was claimed to be density-independent in high density populations with minor growth variation located on the flat, right-side wing of the curve (Egglishaw and Shackley 1977; Mortensen 1977; Elliott 1994). Moreover, identifying the life stage upon which density operated also required census replications with a resolution sufficient to permit the analysis of short periods of growth over successive year classes and sufficient environmental variability during the study years to capture the limits of variation in growth and density (Jenkins et al. 1999).

Conceptual arguments (Cowan et al. 2000), observational assessments (Crisp 1993; Elliott 1994; Jenkins et al. 1999), and experimental studies (Bohlin et al. 2002) have suggested that competition and density-dependent growth are more likely to occur in juvenile stages that are more susceptible to increased intracohort (Jenkins et al. 1999) or intercohort (Crisp 1993) densities. This contrasts markedly with the results of this study where density showed potential to operate on any life stage (i.e., site S1). The specific life stage, the ranges of density upon which density operated, and the relative importance of intra- and inter-cohort density varied greatly among sites. Decreased cohort-specific mass with increased density showed that stronger year classes bring about reduced growth at a site scale (except at site S4). Negative effects of cohort density concurred with persistent effects of intra- and inter-cohort densities over successive life stages (i.e., S1 and S2), whereas these effects were non-apparent at site S4 where the operation of density over life stages was negligible.

Factors and mechanisms responsible for site-specific growth–density relationships

Growth and mortality are deemed independent processes upon which density might operate and whose operation may translate into each other process. Density-dependent competition occurs when food is limited and (or) the habitat is saturated by individual territories (Grant and Kramer 1990), resulting in reduced individual feeding rates (Heath 1992). Several studies have documented density-dependent mortality in the absence of density-dependent growth (McFadden et al. 1967; Mortensen 1977; Elliott 1994) or density-

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dependent growth when mortality was density-independent (Jenkins et al. 1999; Bohlin et al. 2002). This is dissatisfying because if the operation of density results in reduced food intake (Heath 1992), density-dependent growth should necessary occur before density-dependent mortality.

For the same cohorts and sites of this study, Rincón and Lobón-Cerviá (2002) and Lobón-Cerviá (2003) described an initial phase with negligible or no mortality followed by a steep trajectory of severe decline. Rincón and Lobón-Cerviá (2002) advanced that the relationships between per capita resources and brown trout mass depend on the site. Because of size-selective habitat availability at a site scale, larger individuals requiring greater territories face limited deeper waters (i.e., pool habitat), especially when individuals achieve a threshold size (15 cm; 40 g) when the trajectories of mortality and self-thinning switched from negligible to severe.

Relative levels of habitat occupancy support the hypothesis that spatio-temporal variations in space suitable for sized individuals are the immediate factors responsible for the site-specific growth–density patterns. Spatial resources available at the study sites appeared limiting to both growth and survival, with different consequences for different life stages and sites. At sites S1 and S2, where increased food availability permitted faster growth, greater territory size required by larger individuals (Elliot 1990; Keeley and Grant 1995) resulted in a broad occupancy of the site in years of greater recruitment (PHS values for new cohort ≈ 40%), that in combination with the accompanying cohorts forced a fully saturated habitat occupation (PHS values far above 100%). Such magnitudes predict competition within and among cohorts. Apparently, habitat occupancy enhances competition for limited spatial resources sufficient to suppress growth but not enough to induce mortality. A parsimonious explanation is that at high densities, increased competition for territory acquisition may force individuals to broaden the variability of microhabitats to include less favorable ones (Bult et al. 1999), energetically less profitable feeding positions (Fausch 1984), or to feed on less profitable items (Jenkins et al. 1999), resulting in lower brown trout size.

At the larger and deeper site S4 where individuals grew slower and recruitment magnitudes were lower, no intra-cohort effects were detected. A larger area of deeper waters might offer more abundant habitat to less abundant slower growers. Nonetheless, prolonged survival caused by a delay to attain the 15-cm threshold size means that larger (older) individuals of the two accompanying cohorts are always more abundant than the new cohort entering the population. This asymmetry in favor of larger individuals may deplete feeding resources available for juveniles or may favor interference behavior (Grant 1997), where larger individuals may have some advantage to search, detect, and prey during the period of maximum growth (when PHS values attain 47% for combined cohorts).

Once individuals attain ≥15 cm, restricted pool habitat availability intensifies competition. Then, mortality and density-dependent growth occurred simultaneously at all sites.

Influence of other factors on brown trout growth

Temperature and size-selective mortality are frequently cited to influence size-at-age (Elliott 1994). The latter was assumed less relevant for Rio Chaballos brown trout because of negligible mortality during a prolonged period.

The growth rates of life-stage-1 individuals decreased with increasing temperature at three sites (S2, S3, and S4) but were unrelated to temperature at the only site where brown trout mass was related to density (i.e., S1). At other life stages and sites, growth rates were not related to temperature, but brown trout mass was negatively influenced by either intra- or inter-cohort densities. Thus, growth rates were only related to temperature when brown trout mass was unrelated to density and vice versa, suggesting that suppressed growth caused by increased density obscured the effects of temperature on growth rates. Thus, the results of this study, in agreement with Crisp (1993) and Jenkins et al. (1999), suggested that density is a major factor limiting growth in resident, low density populations and further supported its widespread operation as a epiphenomenon capable of obscuring the chronic effect of temperature.

Implications of density-dependent growth for temperature-regulated growth in stream-living brown trout

The tendency of density to obscure the effects of temperature in Rio Chaballos brown trout is consistent with, and makes compatible, the patterns elucidated by studies that have attempted to disentangle the combined effects of density and temperature on growth. With no exception, the studies that identified growth–temperature relationships failed to detect density-dependent growth (Egglishaw and Shackley 1977; Mortensen et al. 1988; Elliott 1994), whereas the studies that identified density-dependent growth failed to detect temperature effects (Le Cren 1973; Crisp 1993; Jenkins et al. 1999). This study added, at least partly, to the latter group. Importantly, these two groups of populations match the upper and lower density ranges upon which density effects on mass are maximized or minimized, respectively. Consistency among patterns suggests that detection of growth–temperature relationships may represent instances of minor effects of density or instances in which density effects may be undetected owing to extremely high densities.

This may conflict with numerous studies that have assigned a predominant role to temperature. Over 40 populations used to test the validity of the growth models of Elliott (1975*a*) and Elliott et al. (1995) suggested a predominant effect of temperature on growth rates (Elliott 1994). Recent studies, however, have described either observed growth rates greater than predicted by the models (Rio Chaballos: Lobón-Cerviá and Rincón 1998; Convict Creek, California: Jenkins et al. 1999) or underestimated growth rates in winter (Nicola and Almodóvar 2003) and in cooler Scandinavian streams (Jensen et al. 2000; Vollestad et al. 2002).

The temperature-based model recently developed by Jensen et al. (2000) to predict latitudinal variations in size-at-age implicitly considers density as a factor limiting growth, but its inclusion into the model only added 0.9% of the total variation in growth rates. This may at least partly be due to the range of densities used by Jensen et al. (2000) (which in turn, constituted a substantial part of the populations previously used to test Elliott's models; Jensen 1990). Jensen et al. (2000) did not provide density data, but larger females in their anadromous populations are recognized to

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produce more abundant offspring (similar to Black Brows Beck; Elliott 1994) that, in combination with a mean mass of juveniles in September equal to 1.1 g (range for 22 populations, 0.22–2.58 g), places all these populations at the lower extreme of the mass–density curve where density effects might go undetected and where density-dependent mortality might be the rule rather than the exception (Milner et al. 2003). Given the potential for density to operate on greater growth – lower density populations, most common across the European continent, and its ability to operate at a site scale, it is questionable that the model of Jensen et al. (2000) predicts consistently latitudinal variations in brown trout growth.

Implications of density-dependent growth for population regulation

Potential exists for numerical regulation of stream salmonids through density-dependent growth (Jenkins et al. 1999; Lorenzen and Enberg 2001). A proposed mechanism is that larger female size at low density produce more abundant, larger eggs that may result in increased survival of more abundant, larger juveniles (Miller et al. 1988) by passing the critical period more rapidly (Elliott 1990).

Stream brown trout populations have provided one example of population regulation through negative, compensatory feedbacks (Elliott 1994). Elliott (1994) argued that his anadromous, high density population was regulated by density-dependent mortality in the absence of density-dependent growth. The resident population of this study differed markedly from the British, anadromous population in that recruitment was determined by density-independent processes related to discharge conditions at the time of emergence (Lobón-Cerviá 2004; Lobón-Cerviá and Rincón 2004). In this environmentally driven population with only 1–2 reproductive age classes, there is a risk of population crash when adverse discharge conditions persist during a few years.

Lobón-Cerviá et al. (1997) described a trade-off between egg size and number related to the growth of brown trout in tributaries of the Rio Esva including Rio Chaballos. This trade-off was extended to the youngest juveniles to suggest that where brown trout grew faster, larger females developed more abundant, smaller eggs and juveniles (Lobón-Cerviá 2000). Current results show that stronger effects of density occurred at sites where individuals grew faster (i.e., sites S1 and S2), that is, where larger females at low densities (or when the population is at risk) would produce more abundant, smaller eggs and juveniles. Clearly, if individuals grew according to temperature (under no density effects), habitat occupation at these two sites of faster growth would increase in years of greater recruitment to levels where competition would inevitably result in mortality. Individuals would attain the 15-cm threshold size at a younger age upon which severe mortality caused by limited habitat availability would restrict survival of individuals to spawn. In turn, a density-dependent delay to attain 15 cm might result in an increasing abundance of survivors such as those observed at site S4.

Nevertheless, are these responses to increased density relevant for the persistence of the population? In Rio Chaballos, density-dependent growth did not translate into density-dependent mortality. Apparently, increased density obscures the effects of temperature to result in a mass–density relationship where mortality is negligible. Thus, the operation of density appears to maintain the population at the greatest possible abundance previously determined by recruitment.

Several studies cast doubt that changes in growth, with consequences on fecundity, might be sufficient to stabilize recruitment (i.e., Craig and Kipling 1983; Koslov 1992). This seems to be the case in the population of Rio Chaballos where increases in female size brought about increased fecundity (Lobón-Cerviá et al. 1997). Nevertheless, annual recruitment will eventually be determined by stream discharge upon which the parental population in terms of female or egg density plays, at best, a minor role (Lobón-Cerviá and Rincón 2004). Consequently, the mechanisms generated by the operation of density actually provide no feedback between the abundance of spawners and recruitment.

Thus, although density-dependent growth may permit brown trout to respond to environmental variability, the conditions under which density-dependent growth may translate into density-dependent mortality to regulate population numbers (Jenkins et al. 1999; Lorenzen and Enberg 2001) are unclear and warrant further research.

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Toxicity and bioaccumulation of tributyltin in *Hyalella azteca* from freshwater harbour sediments in the Great Lakes Basin, Canada

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Abstract: This study was designed to evaluate the risk that tributyltin (TBT) levels in harbour sediments pose to the freshwater invertebrate *Hyalella azteca* and to rank TBT as an environmental concern compared with inorganic metal species. Four-week toxicity tests and 2-week bioaccumulation tests were conducted with sediments collected from five harbours historically contaminated with TBT: Montreal, Kingston, Toronto, Hamilton, and Port Weller. While there was no observable effect of TBT on survival or growth of *H. azteca*, bioaccumulation of TBT exceeded levels expected to cause chronic toxicity in some sediments from Kingston, Montreal, and Port Weller. There was a positive relationship between TBT in *H. azteca* and TBT in sediments ($r^2 = 0.72$), although TBT in field sediments was less bioavailable than in laboratory-spiked sediments. Body concentrations of arsenic, cadmium, chromium, cobalt, lead, manganese, nickel, and thallium were well below levels expected to cause toxicity in *H. azteca*. However, overlying water concentrations of copper and zinc approached or exceeded levels of concern in Toronto, Hamilton, and Port Weller sediments. This research suggests that levels of TBT in harbour sediments may cause chronic toxicity to *H. azteca* and freshwater invertebrate species of similar sensitivity and that copper and zinc also pose a risk at these sites.

Résumé : Notre étude cherche à évaluer le risque posé par les concentrations de tributyltine (TBT) dans les sédiments portuaires à l'invertébré d'eau douce *Hyallela azteca* et de classifier le TBT parmi les produits préoccupants pour l'environnement par rapport aux divers sortes de métaux inorganiques. Nous avons procédé à des tests de toxicité de quatre semaines et des tests de bioamplification de deux semaines en utilisant des sédiments prélevés dans cinq ports contaminés dans le passé par le TBT, Montréal, Kingston, Toronto, Hamilton et Port Weller. Bien qu'il n'y ait pas d'effet visible du TBT sur la survie et la croissance d'*H. azteca*, la bioamplification du TBT dépasse les concentrations qu'on croit capables de causer une toxicité chronique dans certains sédiments en provenance de Kingston, Montréal et Port Weller. Il existe une relation positive entre le TBT dans *H. azteca* et le TBT dans les sédiments ($r^2 = 0,72$), bien que la biodisponibilité du TBT dans les sédiments récoltés dans les ports soit moindre que dans des sédiments de laboratoires enrichis de TBT. Les concentrations corporelles d'arsenic, de cadmium, de chrome, de cobalt, de plomb, de manganèse, de nickel et de thallium chez *H. azteca* sont bien inférieures aux niveaux qu'on croit capables de causer une toxicité chez cet invertébré. Cependant, les concentrations de cuivre et de zinc dans les eaux surnageantes des sédiments provenant de Toronto, Hamilton et Port Weller sont à des niveaux inquiétants. Notre recherche indique les concentrations de TBT dans les sédiments portuaires peuvent causer une toxicité chronique chez *H. azteca* et les autres espèces d'invertébrés d'eau douce à sensibilité semblable et que le zinc et le cuivre posent des risques à ces sites.

[Traduit par la Rédaction]

Introduction

Tributyltin (TBT) compounds are widely used antifouling agents that have been regulated in Canada since 1989 because of both their toxicity to nontarget organisms at low environmental concentrations and their persistence in the environment (e.g., Maguire 2000). Despite these efforts, there is strong evidence that TBT remains a risk to freshwater organisms. Recent Canada-wide surveys of TBT concentrations in water and sediment (Chau et al. 1997*a*; S.P. Batchelor, personal communication), laboratory toxicity tests (Day et al. 1998; Bartlett 2004; Bartlett et al. 2004*b*), and preliminary bioaccumulation data (Borgmann et al. 1996) suggest that environmental levels are high enough to cause chronic toxicity in sensitive freshwater invertebrate species. However, insufficient field bioaccumulation data exist to support or refute this hypothesis.

Several surveys have been conducted to quantify spatial and temporal butyltin contamination in the Canadian aquatic environment by measuring bioaccumulation in mussels, usually *Dreissena polymorpha* (Chau et al. 1997*b*; Regoli et al.

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2001; Yang et al. 2001). The highest levels of bioaccumulation in mussels were found in, or in close proximity to, harbours, marinas, and dry dock facilities (i.e., areas of high TBT use). Although these data are useful in terms of monitoring environmental levels and trends of TBT contamination and assessing the extent of this contamination, to our knowledge, the relationship between bioaccumulation and toxicity in these species has not been established and the risk this accumulation poses to aquatic life has not been evaluated. Furthermore, it has not been established if the response of these organisms is typical of other species of freshwater invertebrates.

Hyalella azteca is a freshwater amphipod that has been used extensively in sediment toxicity tests because of its ubiquitous presence in the freshwater environment, ecological importance, contact with sediment, relative sensitivity to contaminants, and ease of culture in the laboratory (Borgmann and Munawar 1989; Ingersoll et al. 1995). Recent studies have determined that *H. azteca* is an ideal species to use in evaluating the impact of TBT contamination on freshwater invertebrates. First, rates of TBT uptake, depuration, and gut clearance are known; *H. azteca* equilibrated rapidly with environmental concentrations of TBT (Bartlett et al. 2004*a*). Second, TBT caused chronic toxicity in *H. azteca* at environmentally relevant sediment concentrations (Bartlett et al. 2004*b*). Third, the relationship between bioaccumulation and toxicity for TBT in *H. azteca* has been determined (Bartlett et al. 2004*b*) and reflects that of four other freshwater invertebrate species (*Hexagenia limbata*, *Physella gyrina*, *Tubifex tubifex*, *Daphnia magna*; Day et al. 1998; Bartlett 2004). Fourth, preliminary bioaccumulation data indicate that *H. azteca* can be used to predict TBT toxicity in field-collected sediment samples (Borgmann et al. 1996).

The objectives of this study were twofold. The first was to assess TBT risk to natural populations of *H. azteca* and similarly sensitive freshwater invertebrates (e.g., *H. limbata*, *P. gyrina*, *T. tubifex*, and *D. magna*) by comparing the bioaccumulation–toxicity relationship for *H. azteca* using contaminated harbour sediments with that obtained from laboratory tests with spiked sediments. The second was to rank TBT as an environmental concern relative to inorganic metal species in these same harbour sediments. The use of TBT in antifouling paints will be gradually phased out until a complete ban occurs in January 2008 (Pest Management Regulatory Agency 2002). As a result, the use of alternative antifouling agents, many of which contain metals such as copper and zinc, will increase, potentially to levels high enough to cause toxic effects in aquatic organisms.

Materials and methods

Sediment collection

Control sediment was collected during the spring of 2001 from a reference site in Lake Erie, Canada (latitude 42.283°N, longitude 81.816°W), using a box core sampler. The top 10-cm layer was removed from the core samples for subsequent use in sediment tests. This sediment was composed of 14% sand, 49% silt, and 37% clay and contained 2% total organic carbon. Measured trace metal concentrations were <120 mg·kg^{-1} of zinc, <60 mg·kg^{-1} of copper, chromium, cobalt, nickel, and lead, <1 mg·kg^{-1} of cadmium, and <0.1 mg·kg^{-1} of mercury. Concentrations of trace metals and total organic carbon in the control sediment were measured by the Caduceon Environmental Laboratory (Ottawa, Ontario) following procedures outlined by the United States Environmental Protection Agency/Corps of Engineers (US EPA/CE; 1981). Sediment from this location has consistently supported high survival of *H. azteca* in chronic toxicity tests (A.J. Bartlett, personal observation). The sediment was sieved through a 500-µm screen to remove larger indigenous organisms and debris and then was stored in the dark at 5 °C until needed. Density and moisture content of the control sediment after sieving were 1.31 g·mL^{-1} and 50.8%, respectively.

Sediments were collected from five Canadian freshwater harbours (Montreal, Kingston, Toronto, Hamilton, and Port Weller) during the fall of 2002 (Fig. 1; Table 1). These locations were chosen because they contain high levels of TBT (Chau et al. 1997*a*; S.P. Batchelor, personal communication), experience high levels of shipping activity, and were relatively accessible. On 16 October 2002, sediment samples were collected from five sites in the canal just below the exit of Lambert Lock in Montreal and from four sites in the Cataraqui River in Kingston near the Kingston dry dock. Four sites in the Welland Canal below Lock 1 (Port Weller) and four samples from the boat slip located at the foot of Yonge Street (Toronto) were collected on 31 October 2002. The final sediment samples were collected from four sites at the centre of Hamilton harbour on 7 November 2002. One sediment sample was collected from each site (i.e., 21 samples total) using a mini-Ponar grab sampler (sample area of 15.2 cm × 15.2 cm), stored in 1-L polycarbonate containers, and kept in a cool, dark place during transport back to the laboratory (<12 h).

Toxicity and bioaccumulation tests

Hyalella azteca were cultured as described in Borgmann et al. (1989). Cultures and experiments were maintained at 25 °C with a 16 h light – 8 h dark photoperiod, and amphipods were fed finely ground Tetra-Min® (Ulrich Baensch, Melle, Germany) fish food flakes sifted through a 500-µm screen. Burlington city tap water (originating from Lake Ontario, Canada; hardness 130 mg·L^{-1}, alkalinity 90 mg·L^{-1}, pH 7.9–8.6) was dechlorinated by aeration and charcoal filtration and used in all of the cultures and as the overlying water in experiments.

All experiments were conducted in the same manner, the only differences between toxicity and bioaccumulation tests being that the former were initiated with young *H. azteca* and run for a 4-week period and the latter were initiated with adult *H. azteca* and run for a 2-week period. With the exception of the control sediment, experiments were set up within 1 to 3 weeks of sediment collection, with three replicates per sediment sample for each type of test. Harbour sediments were not sieved before being added to test containers. Sediment collected from site 1 in Montreal harbour (M1) was not used in tests because it contained large amounts of shells and debris that made handling difficult. Experiments were conducted in 250-mL glass beakers containing 180 mL of water and 20 mL of sediment, the same conditions used in previously conducted spiked-sediment ex-

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Fig. 1. Map showing the location of harbour sites from which sediments were collected for use in the measurement of the toxicity and bioaccumulation of tributyltin in *Hyalella azteca*.

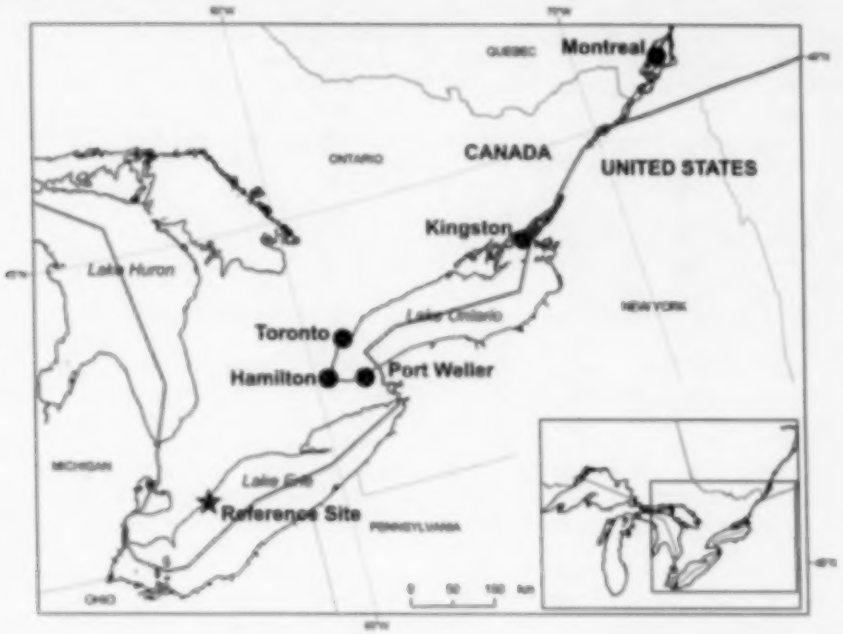

Table 1. Sampling locations of sediments collected for use in tributyltin toxicity and bioaccumulation experiments with *Hyalella azteca*.

Location	Site	Latitude (N)	Longitude (W)	Depth (m)
Montreal	M1[a]	45°30′05″	73°31′09″	10
	M2	45°29′59″	73°31′07″	10
	M3	45°29′53″	73°31′03″	10
	M4	45°29′51″	73°31′02″	10
	M5	45°30′11″	73°31′11″	10
Kingston	K1	44°14′11″	76°28′48″	5
	K2	44°14′10″	76°28′46″	5
	K3	44°14′08″	76°28′45″	5
	K4	44°14′08″	76°28′47″	5
Toronto	T1	43°38′30″	79°22′30″	6
	T2	43°38′26″	79°22′28″	6
	T3	43°38′26″	79°22′26″	7
	T4	43°38′24″	79°22′26″	8
Hamilton	H1	43°17′39″	79°50′36″	22
	H2	43°17′40″	79°50′29″	22
	H3	43°17′36″	79°50′26″	22
	H4	43°17′34″	79°50′28″	22
Port Weller	W1	43°13′08″	79°12′09″	8
	W2	43°13′07″	79°12′09″	8
	W3	43°13′07″	79°12′09″	3
	W4	43°13′08″	79°12′09″	2

[a]Sample not used in experiments.

periments (Bartlett et al. 2004*b*). Water was added to the beakers first, and then sediment was carefully injected onto the bottom using a large plastic syringe with its opening inserted into a plastic tube. In this manner, the bottom surface was evenly covered with sediment with minimal mixing with the overlying water. The beakers were covered and aerated by attaching an air line to the end of a Pasteur pipette and positioning the mouth of the pipette approximately 2 cm above the surface of the sediment. The airflow was adjusted to minimise disturbance of the sediment. The beakers were aerated for 7 days before the addition of animals to allow equilibration of the system and oxygenation of the surface sediment. Time 0 overlying water samples were collected after 6 days of equilibration by carefully decanting 25 mL of water from each of the six replicates per site (three from toxicity and three from bioaccumulation tests) and combining them in 250-mL polycarbonate bottles, giving a 150-mL water sample per site. The water samples were adjusted to pH 2 with concentrated hydrochloric acid and stored in the dark at 5 °C pending chemical analysis. The overlying water removed from the beakers (14% of the total volume) was replaced with clean dechlorinated water.

To initiate 4-week toxicity experiments, twenty 0- to 1-week-old animals were added to each beaker. They were fed ground Tetra-Min in the following amounts: 2.5 mg at the start of week 1, 2.5 mg twice in week 2, 2.5 mg three times in week 3, and 5 mg three times in week 4. Two-week bioaccumulation tests were initiated by adding 20 adult amphipods (5–6 weeks old) to each container. The adults were fed 5 mg of ground Tetra-Min three times each week. Feeding is unlikely to affect TBT bioaccumulation as TBT uptake is primarily through the dissolved phase (Bartlett et al. 2004*a*). Beakers in all tests were gently aerated for the duration of the experiments to ensure that adequate oxygen levels were maintained. Water quality parameters were measured every 2 weeks throughout the experiments. Mean dissolved oxygen concentration was 8.06 $mg \cdot L^{-1}$ (standard deviation

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(SD) = 0.37, range = 7.22–9.33 mg·L^{-1}), mean conductivity was 0.45 mS (SD = 0.07, range = 0.34–0.65 mS), and mean pH was 8.23 (SD = 0.14, range = 7.85–8.56). Ammonia levels remained undetectable (<0.03 mmol·L^{-1}) in all experiments. Evaporative losses that occurred during the experiments were replaced weekly by adding double-distilled water to the test containers.

At the end of the experiments, an overlying water sample from each test container was collected by carefully decanting as much water as possible without disturbing the sediment (110–175 mL) through a 200-µm mesh (to prevent any amphipods from escaping) and was filtered under vacuum through a 0.45-µm cellulose acetate filter to remove suspended particles (e.g., algae, food, sediment). A 10-mL aliquot was transferred to a 15-mL polypropylene test tube, preserved with 100 µL of 70% nitric acid, and stored at room temperature for subsequent metals analysis. The remainder of the overlying water sample was then transferred to a 250-mL polycarbonate bottle, adjusted to pH 2 with concentrated hydrochloric acid, and stored in the dark at 5 °C for analysis of butyltins. Blank samples were prepared in an identical manner using double-distilled water. Amphipods were removed from the sediment by sieving through a 200-µm mesh. They were counted, rinsed three times with clean dechlorinated water, and transferred to polypropylene specimen containers containing 40 mL of ethylenediaminetetraacetic acid (EDTA; 50 µmol·L^{-1}) and 2.5 mg Tetra-Min for 24 h to clear their guts of contaminated sediment (Bartlett et al. 2004*a*). Loss of TBT from *H. azteca* is rapid in the first 24 h and attributed mainly to gut clearance. The true elimination from the body is much lower and has been estimated at about 5%–8% per day (Bartlett et al. 2004*a*). Therefore, to provide a more consistent measure of TBT in the tissues, excluding gut contents, all body concentrations were measured after 24 h gut clearance. Following gut clearance, amphipods from each replicate were weighed as a group (3–20 animals), transferred to glass storage vials, and frozen at –20 °C. Effects of TBT on growth were estimated from final mean body mass measurements, assuming uniform initial body size among test containers. Tissue samples were freeze-dried and then stored at room temperature in the dark until chemical analysis. Sediment samples were collected by transferring 50–100 g of the original sediment remaining from each site to polycarbonate storage containers and were stored at –20 °C in the dark. They were then freeze-dried and ground in preparation for chemical analysis. Two of the Montreal harbour sediment samples (M2 and M5) were passed through an 850-µm sieve to remove shells and other large debris. Sediment samples from each site were analysed in triplicate.

Tributyltin analysis

Procedures for the extraction, derivatization, and cleanup of water, sediment, and tissue samples are described in detail in Bartlett et al. (2004*a*). *Hyalella azteca* from the bioaccumulation experiments were used to measure butyltins because the animals were larger and provided a greater amount of tissue for analysis compared with the toxicity tests. Amphipods from within a replicate were pooled for analysis (10–20 animals, 6–13 mg dry weight). A tripentyltin chloride (TPeTCl in methanol; Sigma-Aldrich, St. Louis, Missouri, USA) surrogate standard was added to each sample before extraction. Organotins were extracted from the sample matrix using 0.1% tropolone in toluene. After a solvent exchange into hexane, the samples were derivatized with ethylmagnesium bromide (3.0 mol·L^{-1} in diethyl ether; Sigma-Aldrich) and injected into a gas chromatograph equipped with a flame photometric detector. Details of the gas chromatograph operating parameters and quality assurance and quality control procedures, which included certified reference materials, are published elsewhere (Bartlett et al. 2004*a*). Quantitation of organotins was based on flame photometric detection values of peak height responses. External standards containing chloride forms of monobutyltin (MBT), dibutyltin (DBT), TBT, and TPeT were derivatized and run on the gas chromatograph – flame photometric detector and were always within 20% of expected values. Samples were quantified based on these external standards and concentrations adjusted for 100% recovery of the surrogate standard, TPeT, in each sample.

Concentrations of organotin species in this paper are reported as Sn: ng Sn·g^{-1} dry weight for sediment and tissue samples and ng Sn·L^{-1} for water samples. These units of measurement can be converted to concentrations of MBT, DBT, and TBT cations by multiplying by 1.48, 1.96, and 2.44, respectively. The limit of detection (LOD) used was three times the noise of the baseline on the flame photometric detector (MBT, 10 pg·µL^{-1}; DBT, 7.5 pg·µL^{-1}; and TBT or TPeT, 6 pg·µL^{-1}; 1000 µL extract ÷ 11–17.5 mL water, 0.25 g sediment (dry weight), or 1.2–2.6 mg tissue (dry weight)). Reagent blanks were analysed for each matrix according to the methods described in Bartlett et al. (2004*a*). Organotin levels were below detection limits in all blank and control samples. Monobutyltin and dibutyltin concentrations were also measured but were not included in the toxicity analysis because most tissue samples contained levels that were below the LOD and MBT and DBT are orders of magnitude less toxic than TBT (Fent 1996; Chau et al. 1997*a*). Any butyltin toxicity in these experiments was assumed to be due to TBT. Recoveries of the surrogate standard (TPeT) ranged from 40% to 115% in overlying water samples (mean = 92%, SD = 11%, n = 168), from 49% to 132% in sediment samples (mean = 91%, SD = 21%, n = 63), and from 37% to 114% in tissue samples (mean = 85%, SD = 12%, n = 66).

Metals analysis

Overlying water and tissue samples were also analysed for 10 metals (arsenic, cadmium, chromium, cobalt, copper, lead, manganese, nickel, thallium, and zinc) using inductively coupled plasma-mass spectroscopy (ICP-MS). To reduce costs of the analysis, only one replicate sample for each matrix per site was analysed, and metals were not measured in harbour sediments. Metals in sediments were not measured because previous research has shown that metal bioaccumulation and toxicity to *H. azteca* is due primarily to dissolved metal and not metal in the sediment (Borgmann (2003) and references therein). Six amphipods per replicate were weighed as a group (0.5–4.0 mg dry weight), transferred to 15-mL polypropylene test tubes, and digested with 150 µL of 70% nitric acid at room temperature for 1 week. Hydrogen peroxide (30%, 120 µL) was then added, and after a further 24 h of digestion, the tissue samples were made up

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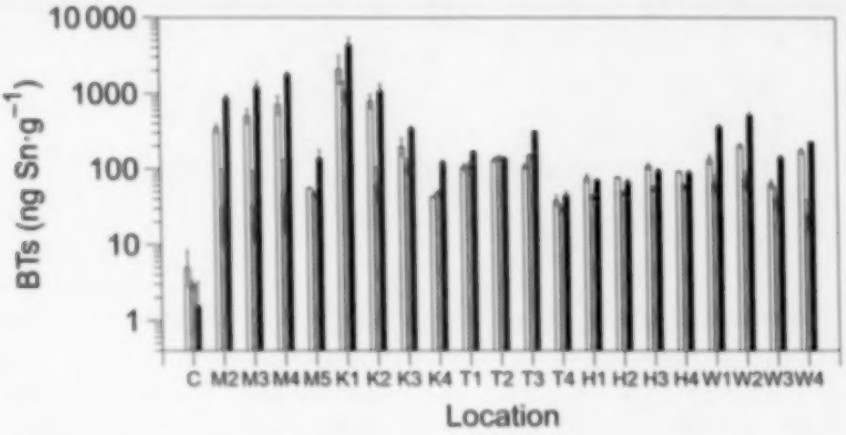
Fig. 2. Butyltins (BTs) measured in control sediments collected from Lake Erie (C) and freshwater harbours contaminated with tributyltin (Montreal (M), Kingston (K), Toronto (T), Hamilton (H), and Port Weller (W)). Open bars, monobutyltin; hatched bars, dibutyltin; solid bars, tributyltin. BTs measured in control sediments were below the limit of detection. Error bars are standard error (n = 3).



to 6.0 mL with double-distilled water. Water and tissue samples were analysed by the National Laboratory for Environmental Testing (Environment Canada, Burlington, Ontario).

Statistical analysis

All statistical analyses were performed using SYSTAT® 8.0 for Windows (SPSS, Chicago, Illinois, USA). Toxicity and bioaccumulation data were based on measured sediment concentrations of TBT because levels in all overlying water samples were below the LOD. Before statistical analysis, survival data were converted to mortality rates (–ln(survival)/time) and then were fourth-root-transformed, and body mass data were logarithmically transformed, to normalize the data and equalize variances. Statistical analysis of the toxicity data was performed by analysis of variance (ANOVA) followed by the Tukey procedure for pairwise comparisons among means. The relationship between bioaccumulation of TBT and sediment concentrations was determined using the NONLIN module, and the data were logarithmically transformed before statistical analysis to normalize the data and equalize variances.

Results

Tributyltin and its degradation products were found at measurable levels in all collected harbour sediments but were below detection limits in control sediments (Fig. 2). Highest concentrations of all measured butyltins were found in Kingston harbour at the site nearest the dry dock facilities (K1). Concentrations of TBT exceeded 4000 ng Sn·g^{-1} in these sediments, DBT was present at about 1000 ng Sn·g^{-1}, and MBT levels were greater than 2000 ng Sn·g^{-1}. Butyltin levels in Kingston sediments decreased rapidly as the distance from the dry dock increased, indicating localised contamination. Concentrations for TBT, DBT, and MBT were lowest at the site sampled in the Cataraqui River just outside the entrance to the dry dock area (K4), measuring 120, 50, and 40 ng Sn·g^{-1}, respectively. Montreal sediments were also contaminated with TBT, with three out of the four sites exceeding 800 ng Sn·g^{-1}. Port Weller sediments were less contaminated; TBT concentrations ranged from 140 to 520 ng Sn·g^{-1}. The highest TBT concentration in Toronto harbour sediments was 310 ng Sn·g^{-1} (T3), and the other three sites all measured less than 170 ng Sn·g^{-1}. Hamilton harbour sediments were the least contaminated with TBT; all sites measured less than 100 ng Sn·g^{-1}. Dibutyltin levels were consistently low in all samples, with the exception of the highly contaminated Kingston site (K1). However, MBT accounted for a substantial proportion of butyltins at sites with high levels of TBT, often exceeding 50% of TBT concentrations. This may be an indication that degradation of TBT (via successive debutylation to DBT and then to MBT) is occurring in these sediments.

Survival and growth of *H. azteca* after a 4-week exposure to TBT-contaminated harbour sediments were expressed relative to location (Table 2) and sediment concentrations of TBT (Figs. 3*a* and 3*b*). Survival was not negatively affected compared with controls in all Montreal sediments (P > 0.70). Survival in Kingston sediments was not significantly lower than controls (P > 0.75), although the lowest survival occurred in K1 (the site closest to the dry dock) and increased slightly as distance from the dry dock increased. The mean number of amphipods remaining in Toronto sediments was less than 60% of controls at all sites, and two replicates of T1 had 100% mortality (significantly different from controls, P = 0.01). Mean survival was less than 60% of controls in two Hamilton sites (H1 and H2, P > 0.79) and in one of the Port Weller sites (W3, P = 0.92); W3 also had one replicate with no survival. Final average body mass (wet weight) of *H. azteca* was variable and showed no obvious trend with location. Body mass was not significantly lower than controls in all sites (P > 0.90) with the exception of M5 (P = 0.02). Indigenous organisms were found in these harbour sediments, although they were unlikely to affect the survival and growth of *H. azteca* because they were not present in sufficient numbers (Reynoldson et al. 1994), they did not represent an additional food source as *H. azteca* graze on algae and detritus on the sediment surface (Day et al. 1998), predatory species were absent, there was no evidence of indigenous *H. azteca*, and survival and growth of *H. azteca*

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Table 2. Data from toxicity tests conducted with freshwater harbour sediments: survival, growth (average final body mass), and tributyltin (TBT) bioaccumulation in *Hyalella azteca* and overlying water concentrations of copper and zinc.

	H. azteca[b]			Overlying water[c]	
Site[a]	Percent survival	Wet mass (mg)	TBT bioaccumulation (ng Sn·g^{-1} dry weight)	Cu (nmol·L^{-1})	Zn (nmol·L^{-1})
C	78.3 (4.60)	1.44 (0.110)	36.0 (8.38)[d]	119	365
M2	81.7 (10.9)	0.953 (0.227)	1100 (167)	137	656
M3	93.3 (4.41)	1.36 (0.0536)	1590 (350)	108	225
M4	86.7 (6.01)	1.02 (0.169)	1680 (98.2)	104	315
M5	91.7 (1.67)	0.517 (0.125)	284 (35.9)	77.8	271
K1	66.7 (18.3)	1.03 (0.318)	2090 (94.7)	197	759
K2	83.3 (1.67)	0.947 (0.253)	516 (42.4)	145	462
K3	88.3 (9.28)	1.03 (0.187)	128 (11.9)[d]	116	764
K4	95.0 (2.89)	1.52 (0.159)	124 (6.20)[d]	71.0	673
T1[e]	18.3 (18.3)	0.900	130 (16.0)[d]	343	—[f]
T2	43.3 (14.8)	1.68 (0.179)	115 (3.20)[d]	285	—[f]
T3	56.7 (6.01)	1.50 (0.138)	244 (5.08)	309	1090
T4	55.0 (7.64)	0.987 (0.389)	73.6 (6.98)[d]	258	289
H1	48.3 (1.67)	1.33 (0.306)	125 (14.3)[d]	262	807
H2	38.3 (7.26)	1.65 (0.410)	117 (7.67)[d]	180	229
H3	70.0 (5.77)	1.43 (0.217)	126 (13.6)[d]	235	2260
H4	60.0 (2.89)	1.94 (0.0762)	119 (11.6)[d]	247	497
W1	63.3 (6.01)	1.80 (0.297)	1080 (34.3)	257	1660
W2	75.0 (2.89)	1.73 (0.205)	1320 (43.3)	249	1880
W3[g]	50.0 (25.0)	1.04 (0.225)	588 (58.7)	277	1060
W4	66.7 (7.26)	1.63 (0.330)	654 (56.0)	258	2290

[a]C, control (Lake Erie); M2–M5, Montreal; K1–K4, Kingston; T1–T4, Toronto; H1–H4, Hamilton; W1–W4, Port Weller.
[b]Data are means of three replicate samples; numbers in parentheses are standard errors (n = 3).
[c]Data are from a single replicate.
[d]Below the limit of detection.
[e]100% mortality in two replicates, n = 1.
[f]Above the limit of detection but less than blank concentrations.
[g]100% mortality in one replicate, n = 2.

were not lower than controls in sediments containing the greatest number of indigenous organisms. Tubificid worms were found in all harbour sediments, with the highest numbers in Port Weller sediments and the lowest numbers in Kingston sediments. Some chironomid larvae were found in Port Weller, Montreal, and Toronto sediments, and a few mayfly larvae were found in Montreal and Port Weller sediments. No relationship between toxicity and levels of TBT could be determined for survival or growth of *H. azteca* (Figs. 3*a* and 3*b*).

Bioaccumulation of TBT in *H. azteca* closely paralleled levels of TBT measured in harbour sediments. Bioaccumulation of TBT could not be compared with TBT concentrations in overlying water because these were below the detection limit owing to limitations in water volumes available for analysis. However, bioaccumulation of TBT is primarily through the dissolved phase (Bartlett et al. 2004*a*). Body concentrations were above 2000 ng Sn·g^{-1} in K1, above 1000 ng Sn·g^{-1} in M2, M3, M4, W1, and W2, and below the LOD in control, K3, K4, T1, T2, T4, and all Hamilton harbour sediments (Table 2). Although MBT and DBT were present in all sediment samples, *H. azteca* did not accumulate these compounds in significant quantities; most tissue samples (97% and 89%, respectively) contained levels that were below the LOD.

There was a strong relationship between levels of TBT accumulated in *H. azteca* and levels in the sediment (solid line, Fig. 4), and it was described well by an allometric model (r^2 = 0.717):

$$C_{BODY} = 10^{0.626}(C_{SED})^{0.782}$$

where C_{BODY} is the concentration of TBT in *H. azteca* and C_{SED} is the concentration of TBT in the sediment. The slope value of <1 (95% confidence interval (CI) = 0.653–0.911) could be due to either a leveling off (saturation) of bioaccumulation at high C_{SED} or a small background C_{BODY} at low C_{SED} (as explained in Bartlett et al. 2004*b*). The relationship between bioaccumulation of TBT in *H. azteca* and sediment TBT concentrations was previously described in chronic toxicity tests conducted with spiked sediments (broken line, Fig. 4; Bartlett et al. 2004*b*). The slope of the regression derived from spiked sediments is similar to that of field sediments (0.862, 95% CI = 0.799–0.926), but the height of the line in the present study (*y* intercept = 0.626) is lower than that of the previous study (*y* intercept = 0.879), suggesting that the bioavailability of TBT from these field-collected sediments is reduced compared with spiked sediments.

The results of the metal analysis of overlying water and tissue samples were compared with published LC25 (lethal

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Fig. 3. (*a*) Percent survival of *Hyalella azteca* after a 4-week exposure to freshwater harbour sediments contaminated with tributyltin (TBT). Controls are represented by solid squares (■). (*b*) Final body mass of *Hyalella azteca* after a 4-week exposure to freshwater harbour sediments contaminated with tributyltin (TBT). Controls are represented by solid squares (■).

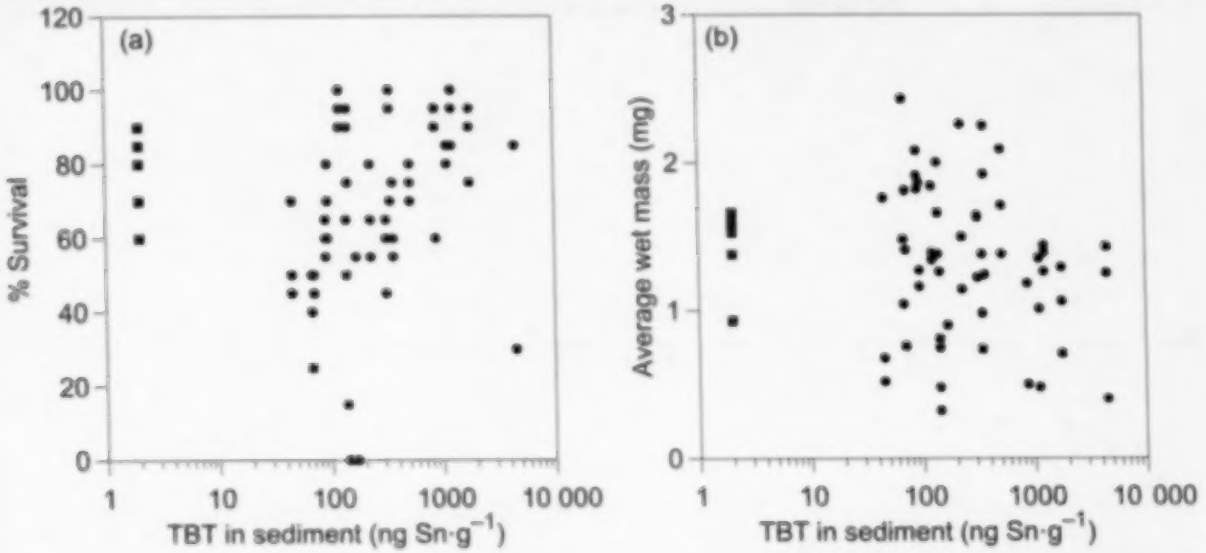
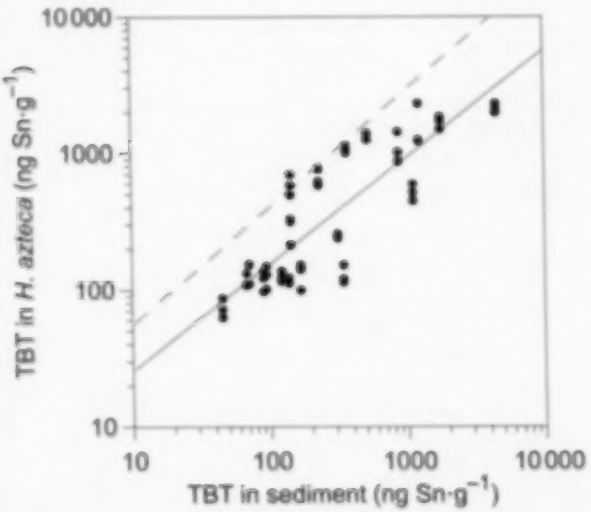


Fig. 4. Bioaccumulation of tributyltin (TBT) by *Hyalella azteca* exposed to freshwater harbour sediments for 2 weeks (solid line, $C_{BODY} = 10^{0.620}[C_{SED}]^{0.782}$). The broken line represents bioaccumulation from spiked-sediment toxicity experiments ($C_{BODY} = 10^{0.870}[C_{SED}]^{0.865}$; Bartlett et al. 2004*b*). C_{BODY}, concentration of TBT in *H. azteca* (ng Sn·g^{-1}); C_{SED}, concentration of TBT in sediment (ng Sn·g^{-1}).



concentration causing 25% mortality) and LBC25 (lethal body concentration causing 25% mortality) values to evaluate the contributions of metal toxicity to organisms in these harbour sediments (Table 3). All overlying water samples were well below the LC25s for arsenic, chromium, cobalt, lead, manganese, nickel, and thallium. Cadmium levels were greater than half of the LC25 in overlying water samples collected from T1, T2, T3, and H4 sediments. Overlying water samples met the LC25 for cadmium in K3 and W3 and exceeded the LC25 for cadmium by 17-fold in T4 and 3.5-fold in H3 samples. However, the toxicological significance of these high cadmium levels is questionable, as bioaccumulation of cadmium from the same samples was well below the LBC25. Copper concentrations were greater than half of the LC25 in Toronto, Hamilton, and Port Weller samples and exceeded the LC25 in T1. Zinc levels were low in most overlying water samples but approached the LC25 in H3 and all of the Port Weller sediments. Tissue samples were below the LBC25 for all metals except for copper; two of the Hamilton harbour sediments resulted in bioaccumulation of copper to 90% of the LBC25. No correlation was apparent between toxicity and copper or zinc concentrations in the overlying water, although the lowest survival (18%) occurred in T1, the same sediments that contained copper levels in excess of the LC25 (Table 2). Neither copper nor zinc was correlated with body concentrations of TBT in *H. azteca* (Table 2).

Discussion

Tributyltin concentrations in sediments

Butyltin compounds are present at significant levels in some Canadian freshwater harbour sediments and, in spite of regulations restricting the use of TBT in antifouling paints, do not appear to be decreasing over time. In fact, maximum concentrations in sediments sampled from Montreal, Kingston, and Port Weller have steadily increased from the 1982–1985 national survey conducted before the introduction of regulations (Maguire et al. 1986), to the 1993–1994 survey conducted to monitor the effectiveness of the regulations (Chau et al. 1997*a*), to the most recent survey conducted in 1999 (S.P. Batchelor, personal communication). Tributyltin levels in the sediments collected in the current

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Table 3. Mean and maximum (max.) concentrations of metals in overlying water (nmol·L^{-1}) and *Hyalella azteca* (nmol·g^{-1} dry weight) after 4-week toxicity tests with freshwater harbour sediments contaminated with tributyltin compared with water (LC25) and body (LBC25) concentrations causing 25% mortality after a 4-week exposure in water-only toxicity tests.

	Highest overlying water concentration				Highest accumulation in *H. azteca*			
Metal	Site	Mean	Max.	LC25	Site	Mean	Max.	LBC25
As	Hamilton	38.5	49.4	4600[a]	Port Weller	23.1	26.1	105[a]
Cd	Toronto	16.2	58.3	3.5[b]	Port Weller	23.4	63.1	270[c]
Co	Hamilton	4.77	5.96	57[a]	Port Weller	4.53	5.30	140[a]
Cr	Kingston	10.1	15.4	280[a]	Hamilton	7.17	19.0	162[a]
Cu	Toronto	299	343	330[b]	Hamilton	1830	2180	2380[c]
Mn	Hamilton	991	3330	34 000[a]	Hamilton	720	1320	19 600[a]
Ni	Hamilton	144	166	443[d]	Hamilton	7.85	9.27	194[c]
Pb	Port Weller	1.56	2.62	42[b]	Toronto	2.17	3.61	126[c]
Tl	Hamilton	0.399	0.421	48[b]	Hamilton	1.82	2.30	290[c]
Zn	Port Weller	1720	2290	1700[b]	Kingston	915	1090	4420[c]

[a] W.P. Norwood (National Water Research Institute, Environment Canada, P.O. Box 5050, 867 Lakeshore Road, Burlington, ON L7R 4A6, personal communication).
[b] Borgmann et al. (1998).
[c] Borgmann et al. (2001*b*).
[d] Borgmann et al. (2001*a*).

study are 1.3-, 2.9-, and 1.8-fold greater than those in the 1999 survey for Montreal, Kingston, and Port Weller sediments, respectively. Concentrations of TBT in Toronto harbour sediments reached their maximum in the 1993–1994 survey, decreased to half of those levels by 1999, and were measured at the same levels recorded in the 1993–1994 survey in this study. Tributyltin levels in Hamilton harbour sediment remained stable between the 1993–1994 and 1999 surveys and decreased 32% between 1999 and 2002. These data suggest that continuing inputs of TBT are occurring in Montreal, Kingston, and Port Weller harbours, Toronto sediments may have received recent inputs of TBT but contamination remains relatively low, and Hamilton sediments are not receiving significant additional TBT contamination. Tributyltin concentrations have also remained stable in freshwater sediments in other countries despite regulations to reduce inputs (Becker-van Slooten and Tarradellas 1995; Fent and Hunn 1995; Traas et al. 1996).

The highest levels of TBT occurred in localised areas of high shipping activity (Montreal, Port Weller) and in close proximity to dry dock facilities (Kingston), i.e., areas of high TBT use. This indicates that stable or increasing levels of TBT are due to legal use on large vessels, dry dock activities and wastewaters, persistence in sediments, and perhaps illegal use on smaller vessels. Localised TBT contamination of sediments has also been reported for the Quebec City harbour area of the St. Lawrence River (Regoli et al. 2001). Concentrations of TBT were highest in sediments of the Bassin Louise marina (888 ng Sn·g^{-1}) and declined sharply within a 1-km distance from the marina. The implementation of the ban on TBT-containing antifouling paints should see a stabilisation and eventual decrease in butyltin sediment concentrations in these contaminated areas.

Potential tributyltin impacts on aquatic biota

Although TBT in harbour sediments remains elevated, its bioavailability at these study sites is less than expected based on previously conducted experiments using laboratory-spiked sediments (Bartlett et al. 2004*b*). Tributyltin was bound to field sediments more strongly than to spiked sediments: levels of TBT diffusing from the sediment into the overlying water were undetectable, bioaccumulation in *H. azteca* was reduced, and no overt toxicity was observed at sediment levels fourfold higher than the 4-week LC25 (Bartlett et al. 2004*b*). Geochemical differences, such as organic carbon content, grain size, and presence of clay minerals (Fent 1996), may have contributed to differences in bioavailability between field sediments and spiked sediments. Reduced bioavailability in field sediments compared with spiked sediments has been observed for metals (Borgmann 2003) and polycyclic aromatic hydrocarbons (Landrum et al. 1992; Kaag et al. 1998), and the bioavailability of organic contaminants is reduced over time in soils (Alexander 1995). Bioavailability decreases with increasing contact time with the sediment or soil, which contributes to the persistence of TBT in sediment as it is less available for degradation by microorganisms (Alexander 1995; Dowson et al. 1993). Chemical extractability also declines with time as the contaminant becomes more strongly bound to the sediment (soil) matrix; however, these decreases occur more slowly than decreases in bioavailability (Landrum et al. 1992; Alexander 1995). This has significant implications in the process of risk assessment, as regulatory decisions based on concentrations from laboratory-spiked sediments will overestimate the risk to natural populations and emphasizes the importance of measuring bioaccumulation and relating body concentrations of the compound(s) of interest to observed toxicity.

Body concentrations are better predictors of toxicity than environmental concentrations of TBT (Meador et al. 1993; Meador 1997), and the bioaccumulation–toxicity relationship established in previously conducted spiked-sediment experiments (Bartlett et al. 2004*b*) can be used to evaluate the risk that TBT poses to natural populations of *H. azteca* (Fig. 5). Bioaccumulation of TBT in *H. azteca* exposed to field harbour sediments was below the 4-week LBC25 (2840 ng Sn·g^{-1}), which would explain the lack of TBT-related toxicity observed in the present study (short-dashed

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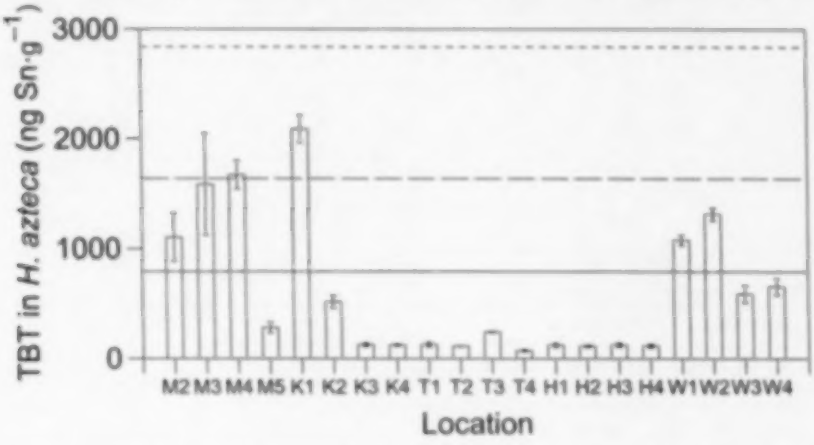
Fig. 5. Risk associated with the bioaccumulation of tributyltin (TBT) by *Hyalella azteca* from contaminated freshwater harbour sediments collected from Montreal (M), Kingston (K), Toronto (T), Hamilton (H), and Port Weller (W). Error bars are standard error ($n = 3$). Horizontal lines represent bioaccumulation associated with toxicity to *H. azteca* after chronic exposure to TBT-spiked sediments. Short- and long-dashed lines are the 4- and 10-week lethal body concentrations associated with 25% mortality, respectively, and the solid line is the 10-week effective body concentration associated with a 50% decrease in reproduction (Bartlett et al. 2004*b*).



line, Fig. 5). However, bioaccumulation from Montreal (M2, M3, M4), Kingston (K1), and Port Weller (W1, W2) sediments approached or exceeded the 10-week LBC25 (1640 ng Sn·g^{-1}; long-dashed line, Fig. 5), and these sediments, as well as additional sites in Kingston (K2) and Port Weller (W3, W4), approached or exceeded the 10-week effective body concentration associated with a 50% decrease in reproduction (EBC50; solid line, Fig. 5). A recently completed multispecies study (Bartlett 2004) showed significant toxic effects of TBT in *H. limbata*, *P. gyrina*, *T. tubifex*, and *D. magna* at tissue concentrations exceeding 2000 ng Sn·g^{-1}; it is likely that sublethal effects in *H. limbata* occur at body concentrations as low as 1100 ng Sn·g^{-1}, similar to levels causing reproductive effects in *H. azteca* (790 ng Sn·g^{-1}; solid line, Fig. 5; Bartlett et al. 2004*b*). These data indicate that localised areas of harbours with persistently high levels of TBT contamination, such as Montreal, Kingston, and Port Weller, may have effects on sensitive endpoints (e.g., reproduction in *H. azteca*) and (or) species (e.g., *H. limbata*). However, the risk of TBT-induced toxicity to freshwater invertebrates in these contaminated areas is likely to decrease as the ban on TBT-containing antifouling paints takes effect.

Although body concentrations are a better indicator of bioavailable TBT and potential impacts than sediment concentrations, risk assessors sometimes need to make decisions when concentrations in sediment are the only data available. The data generated from this study can be used to generate a sediment effect level that is predictive of toxic effects in *H. azteca* by comparing bioaccumulation from field-collected sediments with laboratory-derived critical body concentrations (Borgmann 2003). For example, the most sensitive endpoint for TBT toxicity to *H. azteca* was the concentration resulting in 50% reduction in reproduction (790 ng Sn·g^{-1}; Bartlett et al. 2004*b*). This level of bioaccumulation occurred at a sediment concentration of 803 ng Sn·g^{-1} when *H. azteca* were exposed to field-collected sediment but only at 220 ng Sn·g^{-1} when *H. azteca* were exposed to laboratory-spiked sediments. A reasonable preliminary guideline for an effect level for TBT in freshwater harbour sediments would, therefore, be about 800 ng Sn·g^{-1}, based on current estimates of TBT toxicity to five species of freshwater organisms (Bartlett 2004; Bartlett et al. 2004*b*) and TBT bioavailability in these harbour sediments. Some of the most contaminated harbour sediments exceeded this value. Meador et al. (2002) suggest that TBT levels in the sediment more than 10-fold lower (49 ng Sn·g^{-1}) are necessary to protect estuarine benthic invertebrates from sublethal toxicity. However, if the data are expressed on a tissue concentration basis, a level of 1230 ng Sn·g^{-1} is recommended to protect against adverse effects, which is within the range of concentrations (790–2000 ng Sn·g^{-1}) that causes effects in some species of freshwater invertebrates (Bartlett 2004; Bartlett et al. 2004*b*). This further illustrates the importance of relating effects to bioaccumulation in addition to environmental concentrations.

Comparison of potential tributyltin and inorganic metal impacts

Toxic effects were not associated with TBT or metals measured in this study, and this may be related to factors beyond the scope of this research. Harbours receive a variety of anthropogenic impacts in addition to those associated with antifouling paints. The presence of organic chemicals (e.g., polycyclic aromatic hydrocarbons, polychlorinated biphenyls) and industrial and sewage effluents are contributing elements to the toxicity of harbour sediments. Although it can be difficult to isolate the primary cause(s) of effect in these complex environments, predictions can be made about the contribution that each toxicant makes to the overall toxicity of the sediment by measuring its bioavailability.

Concentrations of metals were measured in the current study in an attempt to rank the issue of TBT with respect to metals contamination and also to evaluate the risk posed by the increased use of metals commonly used in antifouling paint formulations (i.e., copper and zinc). Maximum measured (i.e., bioavailable) concentrations of each metal and

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Table 4. An evaluation of the risk to *Hyalella azteca* posed by metals and tributyltin (TBT) in freshwater harbour sediments by comparing measured (i.e., bioavailable) concentrations to those known to cause toxic effects.

Metal	Measured concentration (nmol·g^{-1} dry weight)[a]	Effect concentration (nmol·g^{-1} dry weight)[b]	Measured/effect concentration
As	23.1	105	0.22
Cd	23.4	270	0.09
Co	4.5	140	0.03
Cr	7.17	162	0.04
Cu	299[c]	330[d]	**0.91**
Mn	720	19 622	0.04
Ni	7.85	194	0.04
Pb	2.17	126	0.02
Tl	1.82	290	0.006
Zn	1720[c]	1700[d]	**1.01**
TBT	2090[e]	2840[f]	**0.74**

[a]Highest mean body concentration (from Table 3).
[b]Body concentrations causing 25% mortality in 4 weeks (from Table 3).
[c]Highest mean overlying water concentration (nmol·L^{-1}, from Table 3).
[d]Overlying water concentrations causing 25% mortality in 4 weeks (nmol·L^{-1}, from Table 3).
[e]Highest mean body concentration (ng Sn·g^{-1} dry weight, from Table 2).
[f]Body concentrations causing 25% mortality (ng Sn·g^{-1} dry weight; Bartlett et al. 2004*b*).

TBT were expressed relative to the corresponding effect concentration (Table 4). Body concentrations were used as a measure of bioavailability in all cases except for copper and zinc, which are regulated by *H. azteca*; therefore, water concentrations of copper and zinc were used because they are more reliable indicators of toxicity than body concentrations (Borgmann and Norwood 1997; Borgmann et al. 2001*b*). Ratios of measured to effect concentration were well below levels expected to cause toxicity in *H. azteca* in all metals except for copper and zinc (Table 4). Copper (0.91) and zinc (1.01) were present at higher measured concentrations relative to effect concentrations than TBT (0.74). However, the tests reported here were conducted with a 10:1 water to sediment ratio to be consistent with previously conducted spiked-sediment experiments (Bartlett et al. 2004*b*). Overestimation of bioavailable copper and zinc under these conditions is possible, as overlying water concentrations are a better indicator of bioavailable metal if tests are conducted with a high (67:1) water to sediment ratio (Borgmann et al. 2001*a*).

Because of the ban on TBT-containing antifouling paints, the risk of TBT to freshwater invertebrates will decrease as no new contamination is introduced into the aquatic environment and degradation processes (both abiotic and biotic) continue to occur. However, the concomitant increase in the use of copper and zinc as antifouling agents will create new problems, as environmental levels in some harbour sediments may already be high enough to cause chronic effects in *H. azteca* and will likely continue to increase. When TBT regulations were introduced in France in 1982, consumers switched to antifouling paints containing copper oxide as the biocidal component. Increased bioaccumulation of copper in oysters reflected this increased use of copper-based antifouling paints (Claisse and Alzieu 1993). Concerns have also been raised about the potential synergistic effects of copper and other "booster" biocides. Dithiocarbamates, a group of alternative antifouling compounds, were one to two orders of magnitude more toxic to a ciliate species in the presence of copper than alone (Evans et al. 2000). Little is known about the acute or chronic effects of the many alternative antifoulants currently in use; the global market share of non-TBT products increased from 2% to 16% between 1988 and 1993, and some booster biocides are now at measurable levels in the environment (Evans et al. 2000).

In conclusion, tributyltin in Canadian freshwater harbours does not appear to be a major environmental concern because significant butyltin contamination was found only in localised areas of high use, i.e., locations with extensive shipping activity (Montreal, Port Weller) or in close proximity to dry dock areas (Kingston), no observed toxic effects occurred in *H. azteca* after a 4-week exposure to contaminated harbour sediments, and TBT in these field sediments was less bioavailable than in laboratory-spiked sediments. However, current levels of TBT in contaminated areas of Montreal, Kingston, and Port Weller harbours could have effects on sensitive species and endpoints. The bioaccumulation–toxicity relationship for TBT in *H. azteca* can be used to predict the potential toxicity of TBT in environmental samples and to monitor the effects of legislation implemented to reduce levels of TBT. A reasonable interim guideline for an effect level for TBT in freshwater harbour sediments would be about 800 ng Sn·g^{-1}. Copper and zinc, present in alternative antifouling agents, are currently at levels that might cause chronic toxicity in *H. azteca*.

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Regional, watershed, and site-specific environmental influences on fish assemblage structure and function in western Lake Superior tributaries

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Abstract: The relative importance of regional, watershed, and in-stream environmental factors on fish assemblage structure and function was investigated in western Lake Superior tributaries. We selected 48 second- and third-order watersheds from two hydrogeomorphic regions to examine fish assemblage response to differences in forest fragmentation, watershed storage, and a number of other watershed, riparian, and in-stream habitat conditions. Although a variety of regional, fragmentation, and storage-related factors had significant influences on the fish assemblages, water temperature appeared to be the single most important environmental factor. We found lower water temperatures and trout–sculpin assemblages at lower fragmentation sites and higher temperatures and minnow–sucker–darter assemblages as storage increased. Factors related to riparian shading and flow separated brook trout streams from brown trout (*Salmo trutta*) – rainbow trout (*Oncorhynchus mykiss*) streams. Functionally, fish assemblages at lower fragmentation sites were dominated by cold-water fishes that had low silt tolerance and preferred moderate current speeds, while fishes with higher silt tolerances, warmer temperature preferences, and weaker sustained swimming capabilities were most common at higher storage sites. Our results suggest that site-specific environmental conditions are highly dependent on regional- and watershed-scale characters and that a combination of these factors operates in concert to influence the structure and function of stream fish assemblages.

Résumé : Nous avons déterminé l'importance relative des facteurs environnementaux de la région, du bassin versant et du cours d'eau lui-même sur la structure et le fonctionnement de communautés de poissons dans des tributaires de la région occidentale du lac Supérieur. Nous avons choisi 48 bassins versants d'ordres 2 et 3 dans deux régions hydrogéomorphologiques afin d'étudier la réponse des communautés de poissons à des différences de fragmentation des forêts, de rétention des bassins versants et de plusieurs autres conditions de l'habitat reliées au bassin versant, à la rive et au cours d'eau. Bien que plusieurs facteurs associés à la région, à la fragmentation et à la rétention aient une influence significative sur les communautés de poissons, la température semble être le facteur environnemental unique le plus important. Dans les sites de fragmentation réduite, les températures de l'eau sont plus basses et la communauté de salmonidés et de chabots prédomine, alors que lorsque la rétention augmente, les températures sont plus élevées et la communauté de ménés, de meuniers et de dards domine. Les facteurs reliés à l'ombrage des rives et au débit permettent de séparer les cours d'eau à ombles de fontaines des cours d'eau à truites brunes (*Salmo trutta*) et arc-en-ciel (*Oncorhynchus mykiss*). Dans les sites de fragmentation plus faible, la communauté de poissons est dominée fonctionnellement par des poissons d'eau froide, à faible tolérance de l'envasement et avec une préférence pour les courants moyens, alors que les poissons qui tolèrent plus l'envasement, qui préfèrent les eaux plus chaudes et qui possèdent des capacités de nage soutenue plus faibles se retrouvent plus communément dans des sites de rétention plus grande. Nos résultats indiquent que les conditions du milieu reliées au site dépendent fortement des caractéristiques qui existent aux échelles de la région et du bassin versant et qu'une combinaison de ces facteurs agissent de concert pour affecter la structure et le fonctionnement des communautés de poissons d'eau courante.

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Introduction

Ecological linkages among landscape features, in-stream habitat, and fish assemblages have not been as thoroughly examined as direct relationships between fish and their in-stream habitats (Gorman and Karr 1978; Angermeier and Schlosser 1989). However, studies on the role of landscape-scale processes (Sharma and Hilborn 2001; Wiley et al. 2002) have led to an improved understanding of the impacts of watershed disturbances across a wide range of spatial scales that influence biotic assemblages (Angermeier and Winston 1999; Schlieger 2000; Wang et al. 2003). One of the primary landscape disturbances in the northern Great Lakes region continues to be logging and land-clearing activities (Johnston 1990). In fact, logging and land clearing have been one of the most significant sources of stress to aquatic ecosystems of the northern Great Lakes for almost two centuries (Government of Canada and US Environmental Protection Agency 1995), and nearly all watersheds in the Lake Superior region were clearcut at least once in the last 125 years (Albert 1995). The effects of logging and associated forest fragmentation on salmonid fishes and their in-stream habitats have been intensively studied in the Pacific Northwest (see Murphy (1995) and Spence et al. (1996) for reviews) but virtually ignored in the midwest. Impacts on western salmonids have been observed; however, responses have not been unequivocal and vary with harvest type (Bisson and Sedell 1984; Hartman et al. 1996). Because of the complexity of these responses in the west, a paucity of data from the midwest, and regional differences in driving climatic factors that may constrain fish assemblages, we examined the ecological impacts of forest fragmentation on fishes in western Lake Superior tributaries. By moving beyond the primarily single population focus taken in the west, we hoped to provide a more holistic view of this issue.

As part of a comparative watershed project in the western basin of Lake Superior, we assessed the vulnerability of streams to landscape disturbance. The overall goal of the broader study (Detenbeck et al. 2000) was to examine differences in hydrology, water quality, and in-stream biotic communities across landscapes with varying conditions of watershed storage capacity and anthropogenic disturbance. Predictions based on a conceptual model were that nutrient and sediment loading, runoff, and stream temperature would increase at higher watershed fragmentation levels (Detenbeck et al. 2000) and that the distribution and quantity of wetlands and lakes in watersheds would mediate some forest fragmentation effects by retaining or processing nutrients, moderating peak flows, and stabilizing baseflow periods (Johnston et al. 1990; Detenbeck et al. 1993). We had three main objectives in this paper: (*i*) to determine the relative influence of hydrogeomorphic region, forest fragmentation, watershed storage, and in-stream habitat on fish assemblages in western Lake Superior tributaries, (*ii*) to gain a better understanding of the interrelationships among landscape and in-stream variables, and (*iii*) to identify which structural and functional characters of the fish assemblages were most indicative of particular environmental conditions associated with our landscape treatments. In a closely related paper (Brazner et al. 2004), we built predictive models that characterized direct linkages between landscape features and fish assemblage characteristics and estimated thresholds in landscape features where dramatic shifts in biotic assemblages were likely to occur. Our focus here is on interrelationships across spatial scales rather than direct linkages per se.

We used both a taxonomic approach and a functional approach to analyze our fish assemblage data because we felt that a functional perspective would provide a more comparable characterization of assemblage response to environmental gradients when assemblages were naturally dissimilar in taxonomy owing to large geographic separation (Keddy 1992; Poff 1997). Our specific expectations about fish assemblage responses were as follows: (*i*) trophic and habitat generalists with warmer water temperature preferences, high silt tolerances, smaller, streamlined body types, and opportunistic spawning strategies that do not require gravel–cobble substrates would be associated with more fragmented watersheds (Schlosser 1982, 1990; Poff and Allan 1995), (*ii*) salmonid species would dominate at colder, less fragmented streams (Barton et al. 1985; Steedman 1988), and (*iii*) cyprinid species would dominate at warmer, more fragmented streams and in streams with higher watershed storage (Lyons 1992*a*; Wang et al. 1997). Because our watersheds included several ecological units with different geomorphologies, vegetation, and climate (Albert 1995), we also anticipated regional differences in biotic responses (Hughes et al. 1987; Wiley et al. 1997) to differences in fragmentation and storage.

Materials and methods

Study area

Our study was completed within 160 km of Duluth, Minnesota, in the Northern Lakes and Forests Ecoregion (Omernik and Gallant 1988) but may be better defined by the US Forest Service ecological unit system (Maxwell et al. 1995), which is based on finer differences in geomorphology, soils, and climate within this ecoregion (Fig. 1). We focused our watershed selection primarily within two ecological units, the North Shore Highlands (north shore streams) and the Lake Superior Clay Plain (south shore streams) (Keys et al. 1995), which provided an excellent contrast in hydrogeomorphic types.

The North Shore Highlands are typified by steeper, rockier, more flashy streams and relatively small watersheds, while streams in the Lake Superior Clay Plain are typically low-gradient, meandering systems with sand and clay soils that contribute to high suspended sediment loads. Wetlands are more common in the headwaters than in the steep, rocky lower reaches of north shore rivers, in contrast with the south shore where wetlands are common in lower stream reaches because of the low gradients. There is more agriculture in south shore watersheds than along the north shore and forestry operations throughout the region. The presettlement forests of both of these areas were dominated by mixed hardwood–pine forests. In the Clay Plain of Wisconsin, balsam fir, white spruce, and sugar maple were the dominant species, but now, trembling aspen dominates with only remnants of the presettlement conifers and hardwoods remaining. In the North Shore Highlands, white pine – red pine, aspen–birch, and mixed hardwood–pine were the dominant presettlement forests, but now, trembling aspen dominate

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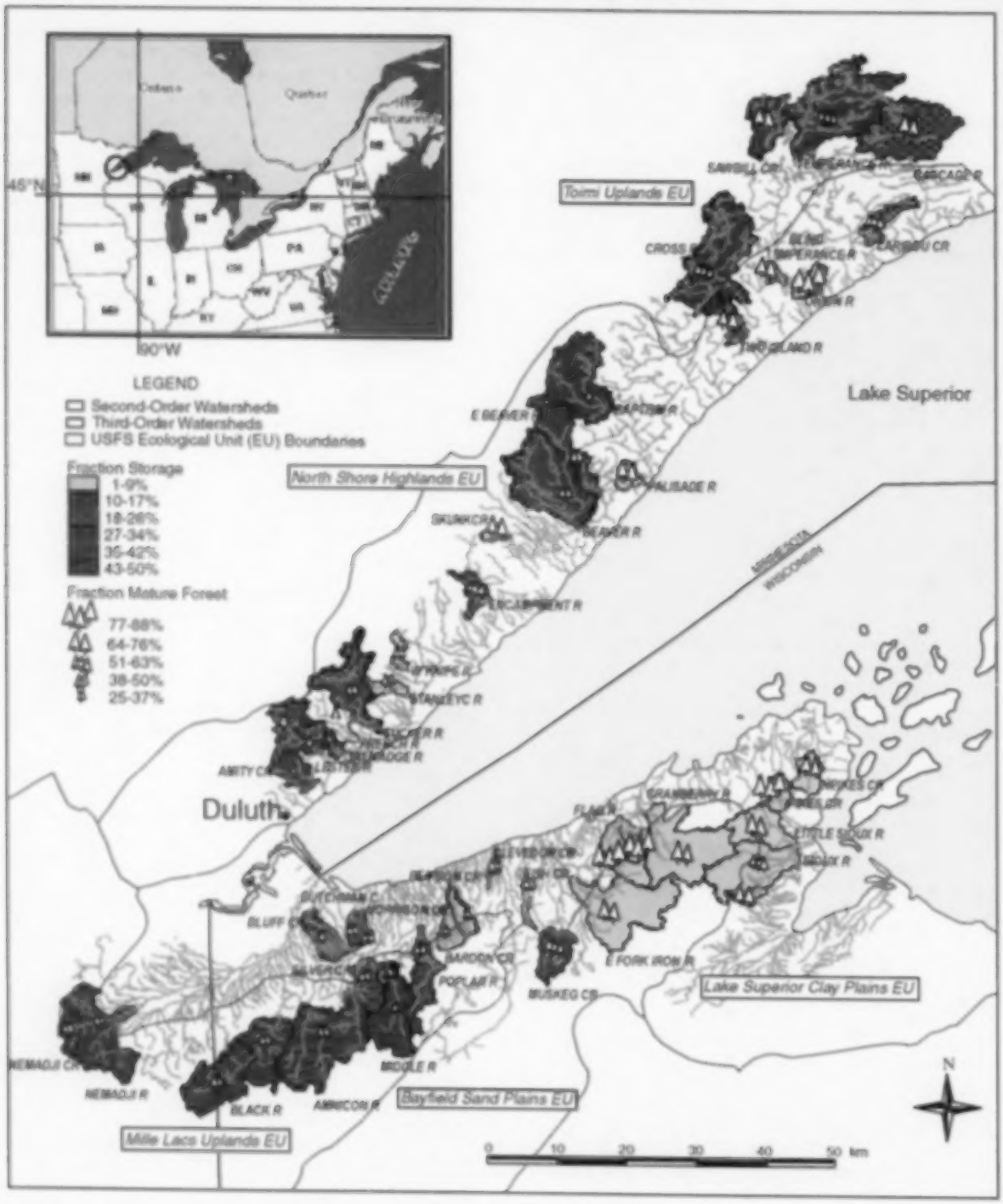
Fig. 1. Map of the comparative watershed study area and its relative position in the Great Lakes.



and balsam fir, white birch, and white spruce are common (Albert 1995).

Our method for describing the population of potential second- and third-order-study watersheds from within these two hydrogeomorphic regions using digital geographic data has been described in detail (Detenbeck et al. 2000). All second- (n = 362) and third-order (n = 90) watersheds in each region within the study area were characterized for

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size, gradient, percent mature forest (>15-year-old stands based on the classification of Wolter et al. (1995)), area recently logged (within the last 15 years based on the classification of Verry (1986)), and storage (total wetland and lake area). Initial selection of 24 second-order and 24 third-order watersheds was a random draw from within the entire population of watersheds to provide a balanced factorial design for two levels of each treatment factor (north versus south hydrogeomorphic region, high versus low mature forest, as a surrogate for forest fragmentation, and low versus high watershed storage) based on estimates from the initial geographic information system (GIS) characterizations of the entire watersheds. Experimental thresholds (50% mature forest, 10% storage) were selected based on hydrologic thresholds related to forest (Verry 1986) and wetland (Hey and Wickencamp 1996) cover established empirically for midwest watersheds. Since the range of watershed storage was quite limited for third-order streams along the north shore, we made an a priori decision to select more south (14) than north shore (10) third-order watersheds to maximize the gradient of storage conditions included. The limited range of storage conditions represented on the north shore obviously limits our ability to draw conclusions about low storage sites on that shore, but since truly low storage watersheds do not occur on the north shore, the problem does not seem particularly important. Nevertheless, readers should keep in mind that owing to these natural landscape constraints, effects related to low storage were derived primarily from changes detected at south shore sites, especially for third-order streams.

In-stream monitoring: physical–chemical conditions

We relied heavily on the habitat evaluation methods and the rationale described by Simonson et al. (1994*a*, 1994*b*) to develop our habitat sampling procedures. We selected habitat and water quality measurements for their potential to influence fish assemblages or reflect watershed conditions. Habitat variables were measured once during August at or near baseflow conditions along a stream reach length of approximately 35 mean stream widths. Habitat and water quality were assessed in 1997 in second-order streams and in 1998 in third-order streams.

Reaches were selected that had in-stream physical habitat, bank vegetation, and land-use characteristics representative of the stream segment of interest based on field reconnaissance of reaches at all possible access points prior to final site selection. We felt that this would help assure that results applied more broadly than simply to the specific reach sampled. Lack of landowner permission and stream inaccessibility limited our ability to do to complete reach assessments for a few streams, but this was generally not a problem. Where sampling reaches were immediately adjacent to road crossings, we selected reaches upstream from the crossing whenever landowner permission allowed. Reaches with permanent tributaries or hydraulic controls (e.g., dams, bridge abutments, and waterfalls) were avoided, as were portions of the stream within 10 mean stream widths of any of these features. Minimum reach length was 150 m and maximum length was 500 m following the rationale of Meador et al. (1993*a*). A random sequence of sampling across all sites was used to minimize potential seasonality effects.

Habitat variables were measured along 13 equally spaced transects per reach, perpendicular to stream flow, as described by Platts et al. (1983) and modified by Simonson et al. (1994*a*). Stream habitat characteristics were measured at either a transect-reach scale (1 mean stream width above and below the transect), a transect-line scale (length or distance of a character along the transect), or at quadrat points (0.3 m × 0.3 m) along the transect lines or based on maps of habitat units made during initial site inspections (Simonson et al. 1994*a*).

Of the 50 in-stream habitat variables that we measured (Appendix A), only a few are not described in Simonson et al. (1994*a*, 1994*b*). Most are self-explanatory, but a few need further detail. Fish cover was defined as habitat features that were at least 0.2 m^3 in volume in or within 0.1 m of water that is 0.05 m deep. We reduced the volume suggested by Simonson et al. (1994*b*) to better reflect habitat for both game (e.g., trout) and nongame fishes (e.g., minnows). Riparian land use was evaluated within 10 m of the stream (instead of 5 m) on both banks, and riparian buffer width was estimated to within 30 m (increased from 10 m). Percent shading in the riparian and percent riparian conifers were visually estimated within 30 m of the stream. The 1- to 3-year floodplain was estimated to a maximum of 50 m along each bank and canopy angle was measured as described in Meador et al. (1993*b*). Habitat complexity was estimated as the total time fished in a reach standardized by the area sampled, since all habitats were fished in a reach and more complex habitats required more time to fish thoroughly.

Water quality conditions (Appendix A) were assessed with a variety of methods. Conductivity and dissolved oxygen were measured with Hydrolab Data Sonde III surveyor probes (Hydrolab Corp., Austin, Texas) in situ, and pH and turbidity were analyzed in the laboratory as described in Detenbeck et al. (1997). Samples were collected monthly during baseflow conditions (Detenbeck et al. 1997). All water quality variables were summarized as mean, maximum, and minimum values observed during all sampling periods. Water temperature was recorded every 15 min from May through October using temperature loggers mounted in pools within 5 cm of the bottom near the middle of each reach (Optic StowAway) (Onset Corp., Pocasset, Massachusetts). Because we were not certain which temporal scale would be most critical for water temperature, it was summarized as 7-, 21-, and 28-day average maximums of continuously logged temperatures and 1-day average maximums. The 1-day average maximum represents the one day during our study with the highest average temperature across the whole day. Maximum averages represent 7- to 28-day periods with the highest average of daily maximum temperatures based on calculations of all possible periods of 7, 21, and 28 days during the study.

Watershed variables

Watershed area, channel gradient, percentage of watershed in mature forest, percent recently logged (≤15 years), and percent lake and wetland cover (Appendix A; Brazner et al. 2002), were quantified using ARC/INFO software (version 7.2) (ESRI, Redlands, California) from GIS data obtained from a variety of sources (Detenbeck et al. 2000). Mature forest cover was quantified as >15-year-old stands using the

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GIS developed by Wolter et al. (1995) from late 1980s Thematic Mapper and Multi-Spectral Scanner satellite imagery. We selected 15 years as our mature forest – recently logged threshold to remain comparable with Verry's (1986) forest classifications for this region. Verry's (1986) analysis indicated that peak flows immediately after snowmelt were significantly higher when the proportion of trees in a watershed <15 years old was >50–60%.

In-stream monitoring: fish assemblages

Fish were sampled using a single upstream pass with towed (larger streams) or backpack (smaller streams) electrofishing gear along a reach length of at least 35 mean stream widths as described for the habitat measurements. This distance typically encompasses three complete pool–riffle or two meander sequences (Leopold et al. 1964) and ensures that the cumulative number of species captured has reached or exceeded an asymptotic level for the stream segment (Lyons 1992*b*; Simonson and Lyons 1995). We used 300- to 500-V DC output pulsed at 60–120 Hz to produce no more than 2.5 A of current to minimize impacts on fish. Effort was made to thoroughly sample all habitats within a reach. Sampling was completed during July and early August when streams were at or near baseflow conditions and within a week or two of when habitat was sampled in a particular reach. All fish >25 mm were identified, counted, and released except for those kept for identification verification. Fish identifications were based primarily on the taxonomic descriptions in Becker (1983).

We also classified all fish by a variety of autecological traits and guilds that we expected might respond to landscape and other environmental differences among our streams (see details in Brazner et al. (2002, 2004)). Swimming and shape factors were calculated as weighted averages per stream based on species quantitative factor values and abundances at each site. All other functional classifications were summarized as the proportion of fish within each class of a particular functional group at a given site. We used proportional rather than absolute abundances because we felt that the relative change in assemblage function in response to differences in environmental factors would be more ecologically informative and comparable across streams with different fish densities.

Data analysis

Ordinations

To assess responses of fish assemblages from western Lake Superior second- and third-order tributaries to regional, watershed, and in-stream environmental gradients and help determine which environmental factors were most important in driving these responses as part of meeting our first study objective, we employed nonmetric multidimensional scaling (NMDS) using PC-ORD software (McCune and Mefford 1997) to ordinate streams in species space. NMDS is an iterative ordination technique based on simple rank similarities among samples that linearizes the relationship between environmental- and species-based distances and effectively identifies responses to multiple environmental gradients (Faith et al. 1987; Clarke 1993).

We used Bray–Curtis dissimilarity as a distance measure to define our sample ranks. Species abundances were $\log(n + 1)$ transformed. We checked for the presence of outliers using methods detailed in McCune and Mefford (1997). This involved comparing the average distance that a particular site is from all other sites with the average distance among all sites. Any site greater than two standard deviations away from the average distance would have been considered an outlier, but we found none. To increase the likelihood of finding optimal solutions to our ordinations, we obtained the starting axes to our NMDS runs from an initial Bray–Curtis ordination of the same data with variance-regression endpoint selection. Only three axes were calculated for each ordination because decreases in stress (a measure of correspondence between dissimilarity in the original space versus distance in the ordination space) were insignificant beyond that point (McCune and Mefford 1997). To evaluate the significance of axes obtained from NMDS runs, we ran Monte Carlo permutation tests (100 simulations) to assess the probability that sample scores in ordination space reflected a more accurate representation of compositional similarity than could be obtained using randomized versions of our data ($p \leq 0.01$) (McCune and Mefford 1997).

Correlations between taxa abundance, functional group proportional abundance, environmental data, and NMDS axes were calculated to help assess which species and environmental variables may have had the strongest influence on differences among sites and how the functional composition of the assemblages varied among sites. Variables that were most highly correlated with the ordination axes were plotted as vector overlays originating from the centroid of the ordination plots. The angle and length of the vectors reflect the direction and strength of the relationship (McCune and Mefford 1997).

NMDS ordinations of streams in environmental space were also completed as another means of evaluating the influence of different environmental factors on differences among streams. Environmental data were relativized by adjusting to the standard deviate for each variable to account for large differences in scale among variable types. Correspondence among species- and environmental-based ordinations was evaluated using a Mantel test, which is a nonparametric test to evaluate the significance of the congruence (positive or negative association) between two dissimilarity matrices with a permutation method (Sokal and Rohlf 1995).

ANCOVA

After field reconnaissance and final site selection, refined GIS characterizations that included only the portions of watersheds above the reaches that were sampled (not completed until months after the field work was completed) indicated that the population of available watersheds in some cases occurred along gradients rather than easily discernable categories as indicated by initial watershed characterizations. Therefore, we used ANCOVA rather than conventional ANOVA to examine the significance of relationships between environmental variables that were highly correlated with streams in species space ordination axes ($r \geq 0.5$) and landscape treatment variables. This was a more quantitative

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method for exploring linkages between landscape and finer scale environmental factors than provided by the ordinations. Identifying and quantifying these linkages was critical to meeting our second objective. We included watershed storage as a covariate in analyses for second-order streams and both watershed storage and percent mature forest as covariates in analyses for third-order streams. Region was evaluated as a main effect for both analyses. Although mature forest – fragmentation classes for second-order streams did not follow perfectly from our threshold selection criteria after GIS refinement (see Brazner et al. 2002), we felt that it was a close enough approximation to continue analyzing these data with mature forest as a categorical variable. One second-order site (Nemadji Creek) that was initially determined to be above the 50% mature forest threshold was actually found to be below it (40% mature forest) after GIS refinement. However, we kept this site in the low-fragmentation class because it had the lowest level of recent logging (1.5%) among all of our study sites (Brazner et al. 2002) and this maintained a balanced design for second-order sites.

Indicator species analysis (ISA)

ISA (Dufrene and Legendre 1997) was used to estimate the significance of relationships between fish species and functional groups that were most strongly correlated ($r \geq 0.5$) with the species-based ordination axes and the landscape treatment factors (hydrogeomorphic region, fragmentation, and watershed storage). The ISAs were needed to meet our third objective of identifying fish species and fish functional groups most indicative of particular conditions in the landscape. The statistical significance of an indicator value was evaluated against Monte Carlo results based on randomized site group assignments (McCune and Mefford 1997). Regional, fragmentation, and watershed storage indicators were calculated. This analysis required categorical assignment of sites to a particular group, so we assigned streams that had ≤50% mature forest to a high-fragmentation group and streams with ≥59% mature forest to a low-fragmentation group for both second- and third-order streams. Because of differences in the distributions of wetland and lake cover, our high- and low-storage categories varied between second- and third-order watersheds. For second-order streams, we assigned all streams with ≤10% watershed storage to a low-storage group and streams with >20% storage to a high-storage group. For third-order streams, <5% was classified as low storage and >15% as high storage.

Results

General environmental conditions

Environmental conditions varied widely among streams (Appendix A) and are most easily summarized in an ordination context (Figs. 2 and 3); however, a few of the differences among sites are worth highlighting. Third-order sites were almost twice as wide but tended to be only slightly deeper and faster than second-order streams at baseflow. Although riparian buffer width was similar at second- and third-order sites, floodplain width was typically two times greater at third-order sites. In contrast, in-stream shade, substrate embeddedness, and average turbidity were all considerably higher at second-order sites. Among watershed variables, area, perimeter, and channel gradient were higher in all third-order watersheds, whereas storage was only higher in north shore watersheds. The streams in the Bayfield Sand Plains (Fig. 1) were distinguished by their low watershed storage, high percent mature forest, cold temperatures, and relatively large quantities of woody debris as fish cover.

Fig. 2. Ordination of second-order streams in species space using nonmetric multidimensional scaling of log fish abundances from sampling in 1997 during the comparative watershed study (proportion of distances among sites in the original data matrix accounted for by the first three axes in ordination space appear as an inset box in Fig. 2*a*; angle and length of vectors radiating from centroid of the ordination reflect the correlation ($r \geq 0.5$) between ordination scores and environmental (italicized characters, broken lines) or fish species (bold characters, solid lines) abundances. Plot of (*a*) axis 1 versus axis 2 and (*b*) axis 1 versus axis 3.

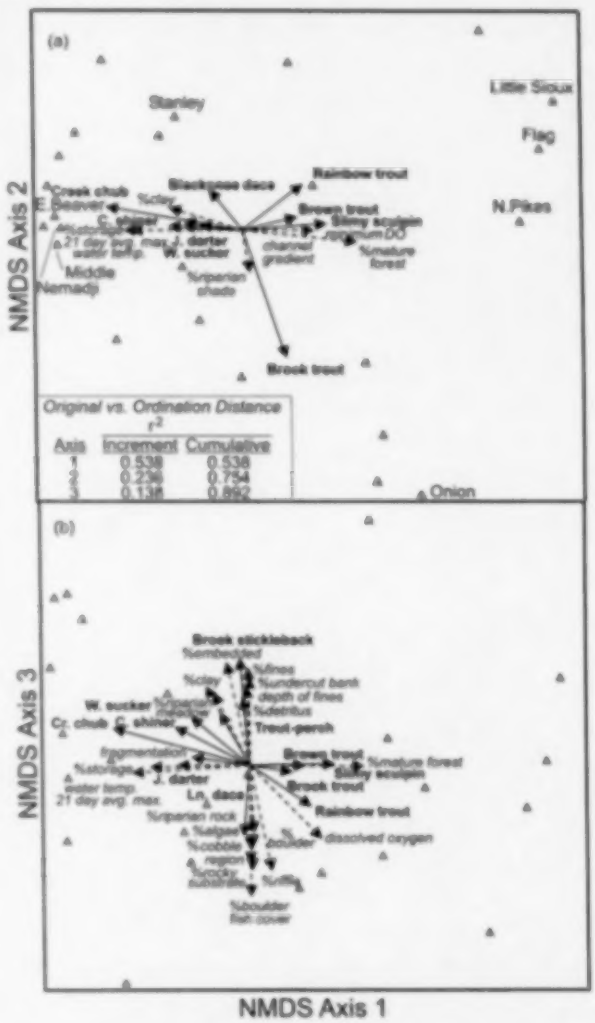

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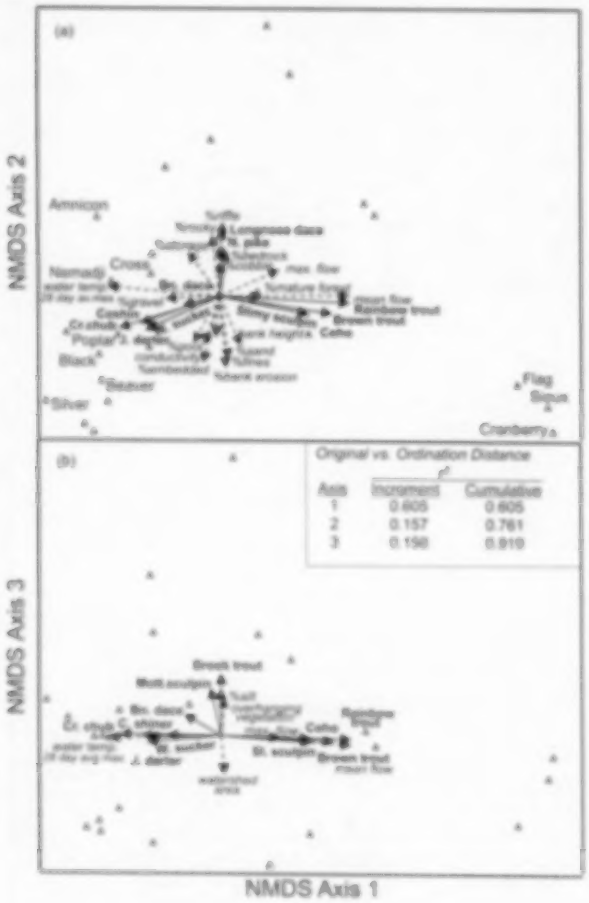
Fig. 3. Ordination of third-order streams in species space using nonmetric multidimensional scaling of log fish abundances from sampling in 1998 during the comparative watershed study (proportion of distances among sites in the original data matrix accounted for by the first three axes in ordination space appear as an inset box in Fig. 3*b*; angle and length of vectors radiating from centroid of the ordination reflect the correlation ($r \geq 0.5$) between ordination scores and environmental (italicized characters, broken lines) or fish species (bold characters, solid lines) abundances. Plot of (*a*) axis 1 versus axis 2 and (*b*) axis 1 versus axis 3.



Streams on the north shore stand out for their high proportion of bedrock and rocky substrates, steep channel gradients, and somewhat higher maximum flows (Appendix A; Brazner et al. 2002).

Fish demographics and assemblage patterns

A total of 4290 individual fish comprising 28 species from 12 families were captured at second-order streams in 1997 and 14 516 individuals comprising 37 species from 13 families were captured at third-order streams in 1998 (for additional details, see Brazner et al. 2002, 2004).

The NMDS solutions for the species-based ordinations on second- and third-order streams provided significantly greater reduction in ordination stress than expected by chance (Monte Carlo permutation tests, $p < 0.01$), indicating that our three-dimensional solutions provide an accurate display of fish assemblage compositional dissimilarity among streams. The percentage of ecological distance among sites accounted for by the first three ordination axes was 89% for second-order streams (Fig. 2) and 92% for third-order streams (Fig. 3), indicating that these ordinations did an excellent job of recovering the ecological complexity of the original distance matrix. Axis 1 accounted for over 50% of the original distance among sites in both ordinations. The patterns apparent in the ordinations were quite similar for both second- and third-order sites. Environmental overlays demonstrate that percent mature forest – fragmentation level, percent watershed storage, water temperature, and flow were key factors associated with separation among our streams along axis 1 (Figs. 2 and 3). Second-order sites located along the upper half of axis 1 (e.g., North Pikes, Flag, Onion, and Little Sioux) were all among the highest in mature forest and coldest in water temperature, while second-order sites located along the lower part of axis 1 (e.g., Nemadji, East Beaver, Middle, and Stanley) typically had high watershed storage, high fragmentation, and warmer water (Fig. 2). Third-order sites along the upper part of axis 1 (Cranberry, Flag, and Sioux) were similar in character to second-order sites along this part of axis 1, except that separation among third-order sites appeared to be driven more by response to flow conditions (Fig. 3). These sites had higher mean and maximum flows compared with third-order sites on the lower part of axis 1 (e.g., Poplar, Black, Beaver, and Silver), which had warmer temperatures and high storage (e.g., Nemadji, Cross, and Amnicon). Salmonids and slimy sculpins (*Cottus cognatus*) were positively correlated with axis 1, while creek chubs (*Semotilus atromaculatus*), common shiners (*Luxilus cornutus*), johnny darters (*Etheostoma nigrum*), and white suckers (*Catostomus commersoni*) were most negatively correlated with it. Functionally, this translated into fishes that require cold water, have low silt tolerances and moderate current preferences, and tend to be large piscivores at sites along the upper portion of axis 1. Small- to medium-sized omnivorous, weaker swimming fishes with cool to warm temperature preferences, slow or general current preferences, and moderate to high silt tolerance characterized sites along the lower portion of axis 1 (Figs. 4 and 5). The strong correlation of percent mature forest and watershed storage with axis 1, which accounted for the majority of variation explained in both ordinations, suggests that each of our watershed treatment factors has an important influence on fish assemblage patterns in the western Lake Superior region. However, since water temperature and flow were strong covariates with these treatment factors and also strongly correlated with axis 1, it is difficult to determine their relative importance.

There was a strong regional signal in both ordinations as well. For second-order streams, it was along axis 3 and for third-order streams, it was along axis 2. South shore sites were characterized by brook sticklebacks (*Culaea inconstans*) and trout-perch (*Percopsis omiscomaycus*), while north shore streams were characterized by longnose dace (*Rhinichthys cataractae*) (Figs. 2*b* and 3*a*) and to some extent rainbow trout (*Oncorhynchus mykiss*) (Fig. 2*b*) and northern pike

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Fig. 4. Ordination of second-order streams with proportional abundances of fish functional groups as overlay vectors. Angle and length of vectors radiating from centroid of the ordination reflect the correlation ($r \geq 0.5$) between ordination scores and functional group abundances. Plot of (*a*) axis 1 versus axis 2 and (*b*) axis 1 versus axis 3.

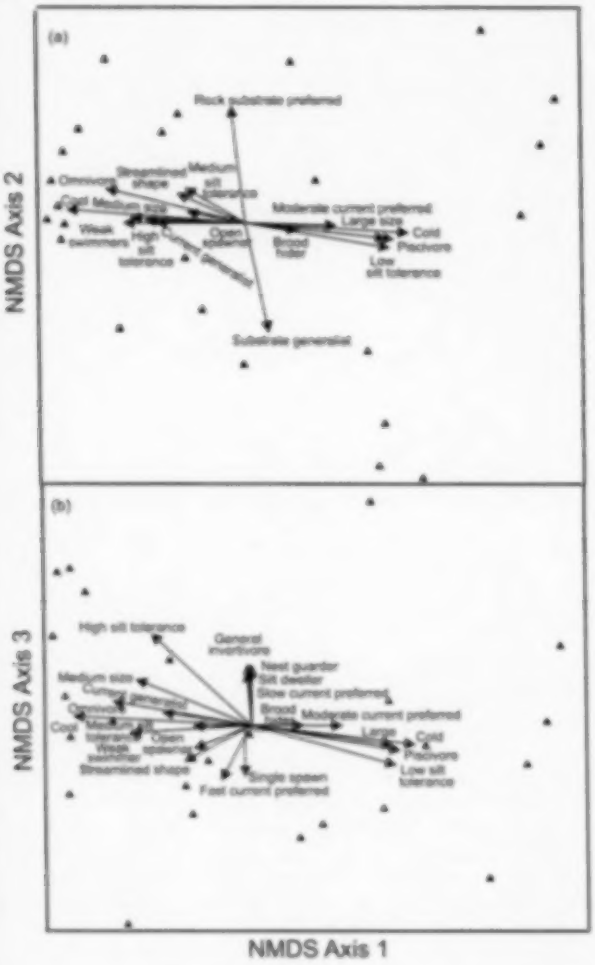
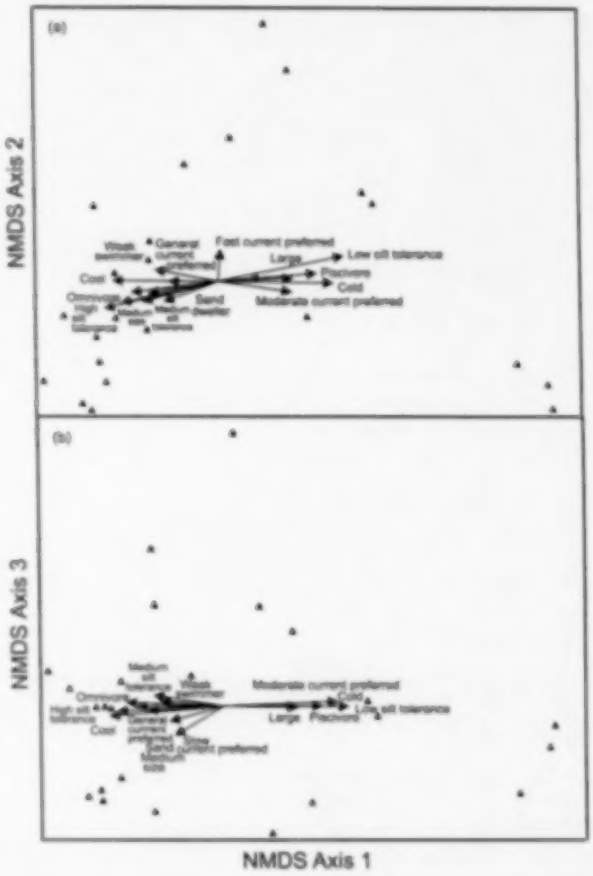


Fig. 5. Ordination of third-order streams with proportional abundances of fish functional groups as overlay vectors. Angle and length of vectors radiating from centroid of the ordination reflect the correlation ($r \geq 0.5$) between ordination scores and functional group abundances. Plot of (*a*) axis 1 versus axis 2 and (*b*) axis 1 versus axis 3.



(*Esox lucius*) (Figs. 3*b*). Functionally, south shore fishes tended to be silt-dwelling, trophic generalists with slow current preferences and a tendency towards nest-guarding spawning behavior (Fig. 4*b*). North shore fishes tended to be single-bout spawners with fast current preferences (Figs. 4*b* and 5*a*). Fine sediments, bank erosion, undercut banks, embedded substrates, and meadow in the riparian were typical habitat conditions associated with south shore sites, while north shore sites were typically rocky, dominated by riffle habitat, and had more prevalent periphyton communities (Figs. 2*b* and 3*a*).

The remaining axis (axis 2, second order; axis 3, third order) in both ordinations was related to differences in brook trout (*Salvelinus fontinalis*). In second-order streams, brook trout streams were separated from other trout and warmwater streams by greater riparian shade, in contrast with streams where blacknose dace (*Rhinichthys atatulus*) were most frequent, which were characterized by more open canopies and higher fragmentation (Fig. 2*a*). The only notable functional characters associated with fishes from these streams were that the brook trout streams were typified by substrate generalists and the dace streams were typified by rock-dwelling fishes. At third-order streams, brook trout occupied streams from smaller watersheds with extensive overhanging vegetation and silty substrates (Fig. 3*b*).

As one means of confirming that the environmental variables most strongly associated with the sites in species space ordinations were among the most important environmental factors in characterizing differences among our streams, we completed sites in environmental space ordinations (all environmental variables included). We compared the ecological distances among sites from these results with the distances among sites derived from the ordinations based on species abundances. We found a highly significant ($p \leq 0.01$) positive association between the environmental-based and the

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Table 1. ANCOVA results for habitat, water quality, riparian, and watershed variables from second-order streams that were highly correlated with sites in species space ordination axes.

					Interaction		
	r	Region (R)	Fragmentation (F)	Storage (ST)	R × F	F × ST	R × F × ST
In-stream habitat							
Fish cover: boulders	0.78	***					
		N > S					
Fish cover: undercut bank	0.64	***				**	
		S > N					
Rocky substrate (%)	0.70	***					
		N > S					
Riffle (%)	0.70	***					
		N > S					
Algae (%)	0.62	***					
		N > S					
Embeddedness (%)	0.69	***					
		S > N					
Depth of fines	0.61	***					
		S > N					
Physical–chemical							
Water temperature:	0.77		***	***		**	
21-day average maximum			H > L	H > L			
Dissolved oxygen: minimum	0.60		**				
			L > H				
Riparian–watershed							
Riparian meadow	0.58	**					**
		S > N					
Bank erosion	0.54	***	**	***	**	**	***
		S > N	H > L	L > H			
Channel gradient	0.55			**			
				L > H			

Note: $^{**}p < 0.05$, $^{***}p < 0.01$; codes below *p* values indicate the general direction of the relationship. N, north shore; S, south shore; H, high; L, low; *r*, correlation with ordination axes. Storage was a covariate. R × ST interactions not shown because none was significant.

species-based distance matrices using Mantel's asymptotic approximation (Mantel 1967; Douglas and Endler 1982). This suggests that the main environmental drivers were similar for both ordination types and indicates that many of the same variables were important in structuring both the species-based and the environmental-based ordinations.

Environmental patterns and landscape treatments

Based on ANCOVA results, there were more significant regional differences in environmental variables than fragmentation or storage-related differences at both second- and third-order streams (Tables 1 and 2). The majority of environmental variables examined at second-order (9 of 12) and third-order (9 of 14) streams were significantly different between hydrogeomorphic regions. Percentage of rocky substrates, algal cover, and riffle area were greater at north shore sites, and percent embedded substrates, bank erosion, and percent fines – depth of fine substrates were all greater at south shore sites in both second- and third-order streams.

Variables that were most significantly different at sites with different mature forest – fragmentation levels included water temperature, conductivity, dissolved oxygen, and bank erosion, although responses were dependent on stream order. Water temperature was higher when fragmentation was high or mature forest was lower, but there was an important interaction with storage. When fragmentation was low in second-order streams, water temperature was positively related to storage. However, when fragmentation was high, water temperature was relatively high irrespective of storage level, suggesting that fragmentation had an overriding influence. In third-order watersheds, the influence of forest cover on water temperature varied by region. Along the south shore, streams with more mature forest had lower water temperatures, but this trend was much weaker along the north shore. Conductivity was higher at third-order sites when mature forest was lower (Table 2), dissolved oxygen had higher minimums at low-fragmentation second-order sites (Table 1), and bank erosion was higher when fragmentation was higher in second-order streams. Interactions indicate that bank erosion was less important at second-order sites on the north shore (Table 1). This is not surprising, since north shore sites are typically dominated by rock and much less susceptible to erosive forces.

Variables that were most significantly different at sites with different storage levels were water temperature, bank erosion, conductivity, dissolved oxygen, watershed area, and channel gradient (Tables 1 and 2). Water temperature was higher when storage was higher at both second- and third-order sites. Bank erosion was much higher along second-order streams when storage was low, but interactions suggest

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Table 2. ANCOVA results for habitat, water quality, riparian, and watershed variables from third-order streams that were highly correlated with sites in species space ordination axes.

					Interaction	
	r	Region (R)	Mature forest (MF)	Storage (ST)	R × ST	R × MF
In-stream habitat						
Riffle (%)	0.74	** N > S				
Embeddedness (%)	0.71	*** S > N				
Fine substrates (%)	0.68	*** S > N				
Rocky substrates (%)	0.67	*** N > S				
Gravel (%)	0.56		** L > H			
Algae (%)	0.51	*** N > S				
Physical–chemical						
Mean flow: baseflow	0.86	** N > S				
Water temperature: 28-day average maximum	0.80		** L > H	*** H > L		**
Flow: maximum	0.58	** N > S				**
Conductivity	0.58		*** L > H	*** L > H	**	
Dissolved oxygen: maximum	0.50			** H > L		
Riparian–watershed						
Bank erosion	0.73	*** S > N				**
Watershed area	0.55			** H > L		
Bank height	0.55	*** S > N				

Note: $^{**}p < 0.05$, $^{***}p < 0.01$; codes below p value: indicate the general direction of the relationship. N, north shore; S, south shore; H, high; L, low; *r*, correlation with ordination axes. Mature forest and storage were covariates; therefore, no three-way interations were tested.

that this was less important when fragmentation was low as well. Conductivity was lower at third-order sites when storage was low (Table 2), dissolved oxygen had higher maximums and watershed area was larger for third-order streams from high-storage watersheds (Table 2), and channel gradient was higher in second-order streams from low-storage watersheds (Table 1). So, it is clear that many of the environmental variables that were most closely associated with the ordination results were also significantly associated with landscape treatment variables. However, in some cases, the effects were dependent on interactions among the landscape variables (e.g., relationship of fish cover to mature forest and storage conditions).

ISA

Results from the ISAs were useful in developing biological indicators of watershed condition. It was reassuring that several of the species (brook stickleback, trout-perch, and longnose dace) that were most strongly correlated with the regional axes in the ordinations were among the best regional indicators in our ISAs (Table 3). Similarly, the best fragmentation and storage indicators were also species that were highly correlated with the ordination axes associated with storage and fragmentation; brook trout and slimy sculpins reflected the least degraded forest conditions, and common shiners and mottled sculpins (*Cottus bairdi*) best typified high-storage watersheds.

The ordination results were also validated by indicator analysis from a functional perspective. Most of the same fish functional groups that were highly correlated with the fragmentation – mature forest, region, and storage-associated ordination axes were also the best indicators of these watershed characters in the ISAs. The low-fragmentation indicators (low silt tolerance, cold water preference, large, piscivorous, moderate current preference) and high-fragmentation indicators (medium sized, omnivorous, cool water preference, high silt tolerance) (Table 4) from the ISAs were virtually identical to the functional groups highlighted in the ordination

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Table 3. Results of indicator species analysis (ISA) used to examine significance ($p < 0.05$) of relationships between fish species and landscape factors.

	Second-order streams, 1997		Third-order streams, 1998	
	Indicator species	p	Indicator species	p
Region				
South	Brook stickleback (*Culaea inconstans*)	0.004	Trout-perch (*Percopsis omiscomaycus*)	0.021
	Slimy sculpin (*Cottus cognatus*)	0.039	Johnny darter (*Etheostoma nigrum*)	0.028
	Central mudminnow (*Umbra limi*)	0.054		
North	ns		Longnose dace (*Rhinichthys cataractae*)	0.010
			Brook trout (*Salvelinus fontinalis*)	0.023
Fragmentation				
Low	Brook trout	0.042	Slimy sculpin	0.019
High	Creek chub (*Semotilus atromaculatus*)	0.016	Creek chub	0.001
	Johnny darter	0.027	Johnny darter	0.003
	Blacknose dace (*Rhinichthys atratulus*)	0.043	White sucker (*Catostomus commersoni*)	0.003
			Common shiner (*Luxilus cornutus*)	0.003
			Fathead minnow (*Pimephales promelas*)	0.039
Storage				
Low	Slimy sculpin	0.005	Brown trout (*Salmo trutta*)	0.005
			Slimy sculpin	0.006
			Coho salmon (*Oncorhychus kisutch*)	0.017
High	Common shiner	0.007	Mottled sculpin (*Cottus bairdi*)	0.029
	Mottled sculpin	0.016		
	White sucker	0.044		

Note: See text for definitions of storage and fragmentation classes; ns, no significant species.

Table 4. Results of indicator group analysis used to examine significance ($p < 0.05$) of relationships between fish functional groups and landscape factors.

	Second-order streams, 1997		Third-order streams, 1998	
	Indicator group	p	Indicator group	p
Region				
South	Nest guarders	0.002	Sand dwellers	0.003
	Speleophils	0.007		
	Slow current preference	0.024		
North	Lithophils	0.018	Fast current preference	0.002
	Fast current preference	0.023		
Fragmentation				
Low	Low silt tolerance	0.001	Cold water preference	0.010
	Cold water preference	0.010	Piscivores	0.010
	Large sized	0.011	Moderate current preference	0.014
	Piscivores	0.030	Large sized	0.051
	Moderate current preference	0.041		
High	Medium sized	0.001	Cool water preference	0.002
	Omnivore	0.001	Medium sized	0.010
	Cool water preference	0.001	High silt tolerance	0.010
	High silt tolerance	0.006	Sand dwellers	0.013
	Medium silt tolerance	0.014		
Storage				
Low	Cold water preference	0.027	Moderate current preference	0.046
	Speleophil	0.045		
High	General current preference	0.001	Multiple spawners	0.046
	Cool water preference	0.001	Silt dwellers	0.034
	Open-substrate spawners	0.021	Cool water preference	0.042
	Medium silt preference	0.036	Open-substrate spawner	0.044
	Small sized	0.037	Warm water preference	0.048

Note: See text for definitions of storage and fragmentation classes.

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plots (Figs. 4 and 5). The function-based storage indicators, although similar to groups identified in the ordinations, also identified spelelophils and multiple spawners as good indicators of different storage conditions.

Discussion

Despite all of the complexities involved in conducting a comparative watershed study at the regional scale, we were still able to elucidate a number of important relationships among landscape, habitat, and fish assemblage characters that allowed us to successfully meet most of our objectives. We certainly gained a better understanding of the interrelationships among various landscape and in-stream habitat variables (our second objective), and we were also able to identify species and functional characters of the fish assemblages that were most indicative of particular landscape conditions (our third objective). It was difficult to quantify the relative importance of any one particular scale of process (e.g., local, watershed, regional) because of the strong interdependencies that typically exist among them (e.g., Richards et al. 1996), although the strength of this interdependency can vary from region to region (e.g., Minshall et al. 1983). So, we were not able to fully meet the goal of our first objective which was to determine the relative influence of different environmental factors at multiple spatial scales. However, our results do provide support for a number of the landscape–habitat–biota linkages that we hypothesized and some strong indications about which environmental factors were most important in driving the patterns in fish assemblages that we observed: high watershed storage was associated with higher water temperatures and minnow–sucker–darter assemblages with higher silt tolerances, warmer temperature and general or slow current preferences, and low storage was associated with low fragmentation, cold water temperatures, and salmonid–sculpin assemblages with low silt tolerance, cold water and moderate current preferences, and piscivorous feeding tendencies. We believe that the low storage – low fragmentation association along the south shore was merely a coincidence of the geology of the watersheds that we studied rather than a general landscape pattern that should be expected in other regions (e.g., there is no reason to believe that low fragmentation precludes high storage or vice versa), but the low fragmentation association with colder water and salmonid assemblages is likely a common landscape–biota connection (Steedman 1988; Maret et al. 1997). It appears that watersheds comprised of a high proportion of mature forest have cooler water temperatures and possibly increased ground water influence (Barton et al. 1985), whereas high watershed storage results in higher stream water temperatures by acting as a direct source of warmer water and by moderating flow and increasing water residence time within the stream (Jacques and Lorenz 1988; Krug et al. 1992). The differences in geology between north and south shore watersheds (particularly those in the Bayfield Sand Plains; Maxwell et al. 1995) could have an important influence on the responses of streams to further change in forest cover. Greater groundwater inputs from the sand moraines along the south shore relative to the more bedrock-laden north shore (Albert 1995) suggests that north shore streams will be more susceptible to water temperature rises following additional forest cutting, since groundwater sources are less likely to moderate the effects of decreased shading.

The fact that more environmental variables differed significantly among regions than at sites with different fragmentation or storage levels suggests that underlying geology and soils, and other regionally varying factors (e.g., gradient), probably had the most important role in structuring habitat in and adjacent to our study streams. Although the greatest number of environmental variables differed significantly across hydrogeomorphic regions, there were surprisingly few strong individual species or fish functional group associations with these axes in the ordinations. This indicates that the potential for regionally driven differences in the assemblages, although large, was not fully realized and suggests that our other landscape treatments may have had more important influences on fish assemblage structure and function. These effects were manifest through effects on water temperature, bank erosion, dissolved oxygen, fish cover, and a number of other factors. It appeared that in some circumstances, forest cover had a stronger role in controlling environmental conditions and influencing fish assemblages at a site than watershed storage because when fragmentation was low, the influence of storage on variables such as bank erosion or the occurrence of undercut banks as fish cover was weak or undetectable. So, the relative influence among the landscape treatment variables is dependent on both their interaction with each other and the habitat or fish assemblage character of interest. Developing more predictive models that relate in-stream habitat, water quality, and riparian conditions to landscape factors will be critical for improving our ability to make accurate predictions about the likely effects of land-use change on in-stream biotic conditions. The ordination and ANCOVA results presented here are a first step in this direction.

Our results are interesting in light of other studies that have tried to identify the relative importance of local and regional processes in structuring biotic assemblages. Although there have been relatively few efforts specifically focused on the relative effects of both local and regional processes on the structure and function of biotic assemblages in streams, there seems to be a difference in the balance of control for different assemblage types. Macroinvertebrate and phytobenthos assemblages seem to be more under the proximate control of local factors such as in-stream habitat and substrate (e.g., Richards et al. 1997; Sponseller et al. 2001), whereas fish assemblage patterns seem to be more strongly influenced by watershed and landscape factors (Mensing et al. 1998; Sharma and Hilborn 2001). However, studies have also shown that geology and land use strongly influence in-stream habitat known to be important to fish (Richards et al. 1996; Johnson et al. 1998), again begging the question of proximate versus ultimate cause. In lakes, where more effort has been made to answer this question, a balance of local and regional processes has been found to control both macroinvertebrate and fish assemblages (Tonn et al. 1990; Allen et al. 1999), although Kelso and Minns (1996) concluded that regional influences primarily structured fish assemblages in the Canadian Great Lakes. Wang et al. (2003) concluded that watershed character plays an increasingly important role as human development in the landscape increases. Determining

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the relative influence of landscape and habitat features seems likely to remain a difficult problem because their influences may be inextricably linked in most situations. The biggest challenge may be in finding the landscape measure(s) that best characterizes this linkage, since it seems likely to vary from place to place. We think this issue deserves considerably more attention in future studies of lake and stream biota that use a landscape approach.

We also think that additional effort should be made to understand the response of fish assemblages to logging rather than just the responses of particular populations or groups of fishes. The focus has been almost exclusively oriented toward effects on salmonid populations (Meehan 1991; Spence et al. 1996) or salmonid diversity (Reeves et al. 1993). Although logging has not been a focus, a more landscape-oriented perspective has been adopted by some assemblage-oriented fish ecologists studying effects of various other anthropogenic disturbances (e.g.,Walser and Bart 1999; Schleiger 2000). Many of the current approaches to estimating biotic integrity have included quantification of forest cover and other land uses as integral parts of their studies (e.g., Maret et al. 1997; Wang et al. 2003).

Our results have implications for index of biotic integrity development in this region. They suggest that a finer-scale approach may be important. Ordinations detected considerable variation in fish assemblages across this region, even though our study watersheds were all within one ecoregion (Northern Lakes and Forests; Omernik and Gallant 1988). Since overall differences in fish assemblages were closely associated with the finer-scaled ecological units containing our watersheds, it may be that the classification systems suggested by Maxwell et al. (1995) and Albert (1995) should receive increased attention by resource managers in future efforts to develop indices of biotic integrity or other biocriteria. The results of our ISAs should provide a reasonable set of metrics for initial testing of these sorts of biocriteria.

From a management perspective, our results suggest that both timber management and wetland restoration or degradation decisions will need to be considered by resource managers when fish community health is a concern. For example, increasing percentages of mature forest cover should allow for salmonid–sculpin assemblages to become more prevalent in streams with the potential for cool or cold waters. Similarly, increased wetland cover should allow for a greater predominance of healthy warmwater fish assemblages assuming that other landscape features are not too badly degraded. By understanding the species structure and functional character of an assemblage and its relationship to landscape features, managers should be able to make at least a rough assessment of watershed condition. Lacking fish data, it might be easier to simply characterize forest cover and storage as a first step in identifying which watersheds likely contain streams that are degraded. Our results suggest that although in-stream habitat rehabilitation should continue to be used an important tool to improve biological conditions in streams, restoration efforts will have greater success if the potential interactions with landscape conditions are factored into the decision-making process. In some situations, manipulation of forest cover or watershed storage may have a greater impact on fish assemblage integrity than in-stream habitat improvements.

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Appendix A

Table A1. Mean and range of in-stream habitat, water quality, riparian, and watershed conditions at second- and third-order streams sampled during 1997 and 1998 during the comparative watershed study.

Environmental variable	Second-order sites (1997)		Third-order sites (1998)	
	Mean	Range	Mean	Range
In-stream habitat variables				
Stream width (m)	4.7	2.7–10.1	7.3	2.7–16.7
Bank-full width (m)	10.5	4.8–20.2	15.5	8.8–23.6
Bank height (m)	1.0	0.6–1.3	1.3	0.7–2.0
Bank erosion (%)	35	2–68	37	4–78
Water depth (m)	0.2	0.1–0.5	0.3	0.1–0.6
Thalweg depth (m)	0.6	0.1–1.1	0.8	0.4–1.3
Flow ($m \cdot s^{-1}$)	0.05	0–0.2	0.06	0–0.2
Maximum flow ($m \cdot s^{-1}$)	0.2	0–0.4	0.2	0–0.4
Fish cover (%)				
Undercut banks	1	0–4	0.1	0–0.8
Boulders	10	0–32	12	0–36
Overhanging vegetation	1	0–9	1	0–5
Submerged or floating aquatic vegetation	0.1	0–2	0.2	0–5
Emergent aquatic vegetation	nd	nd	0.2	0–3
Woody debris	3	0–13	2	0–6
Total	16	7–35	15	12–36

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Table A1 (*continued*).

Environmental variable	Second-order sites (1997)		Third-order sites (1998)	
	Mean	Range	Mean	Range
No. of pieces of large wood (>30 cm)	0.2	0–1.0	0.1	0–0.5
No. pieces medium wood (10–30 cm)	1.2	0–3.2	1.0	0–4.0
Periphyton cover (%)	64	0–100	13	0–44
Depth of fine sediments (m)	0.1	0.01–0.3	0.03	0–0.1
Embeddedness (%)	49	11–98	32	1–56
Substrate (%)				
Bedrock	5	0–53	2	0–32
Boulder	20	0–78	11	0–60
Cobble	53	0–97	28	0–56
Gravel	57	0–95	27	7–53
Sand	34	0–100	27	0–87
Silt	4	0–49	1	0–17
Clay	12	0–100	4	0–32
Detritus	1	0–13	1	0–3
Other	2	0–14	nd	nd
Fine sediments (%)	28	0–97	32	0–92
Riffle area (%)	25	0–60	19	0–63
Pool area (%)	42	0–100	48	14–88
Width to depth ratio	19.2	5.9–44.8	18.0	7.9–27.6
Riffle to riffle ratio	8.0	1.8–43.3	8.1	1.4–33.6
Bend to bend ratio	10.6	0.7–36.2	9.8	0.6–65.7
Reach length (m)	185	150–354	264	156–500
Habitat complexity (seconds fished per square metre)	1.7	0.8–2.8	1.5	0.6–3.1
Rocky substrate (%)	71	0–100	67	7–100
Water quality variables				
Conductivity ($\mu S \cdot cm^{-1}$)	137	44–310	163	31–363
Minimum conductivity	78	8–211	148	29–335
Maximum conductivity	198	68–488	175	32–407
Dissolved oxygen ($mg \cdot L^{-1}$)	9.5	7.2–11.0	8.4	0.8–12.2
Minimum dissolved oxygen	8.3	5.1–10.4	7.4	0.8–11.0
Maximum dissolved oxygen	11.1	8.9–15.8	9.7	0.8–17.7
pH	7.5	6.8–8.0	7.6	6.6–8.4
Minimum pH	6.7	6.1–7.4	7.3	5.3–8.0
Maximum pH	8.0	7.0–8.6	7.9	6.7–8.7
Turbidity (NTU)	33	2–424	12	0.5–155
Minimum turbidity	7	1–67	6	0.3–55
Maximum turbidity	137	4–2117	21	0.8–283
Water temperature (°C)				
7-day average maximum	18.4	12.0–24.9	21.2	12.9–24.1
21-day average maximum	17.6	11.7–22.0	20.2	12.5–23.3
28-day average maximum	17.3	11.6–22.0	19.9	12.3–22.5
1-day maximum average	20.5	13.7–25.2	22.8	14.0–26.4
Riparian variables				
Riparian land cover (%)				
Meadow	24	1.5–72	21	2–64
Rock	3	0–17	2	0–22
Shrubs	42	14–80	34	14–80
Forest	29	4–61	41	0.4–84
Wetland	0.3	0–5	0.4	0–5
Other	2	0–17	nd	nd
Riparian buffer width (m)	56.9	39.9–60.0	57.5	48.4–60.0
Floodplain width (m)	27.4	10.5–60.7	54.2	23.3–100.0
Riparian coniferous trees (%)	21	0–49	24	0–65
Riparian shade (%)	50	27–68	40	12–58
In-stream shade (%)	29	6–49	12	1–29
Canopy angle (degrees)	47.4	8.9–94.6	79.7	38.1–145.4

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Table A1 (*concluded*).

Environmental variable	Second-order sites (1997)		Third-order sites (1998)	
	Mean	Range	Mean	Range
Watershed variables				
Storage (% lake and wetland area)	18	1–50	21	1–44
Mature forest cover (%)	53	26–88	50	25–81
Recently logged (%)	15	2–38	11	2–27
Watershed area (km^2)	30.4	6.9–96.6	99.1	21.9–197.2
Watershed perimeter (km)	31.3	15.5–69.8	59.9	24.1–97.2
Channel gradient ($m \cdot km^{-1}$)	10.7	0.9–30.1	17.6	1.2–29.0

Note: See text for explanation of variable measurement, most described in Simonson et al. 1994; nd, not detected; NTU, nephelometric turbidity unit.

Reference

Simonson, T.D., Lyons, J., and Kanehl, P.D. 1994. Quantifying fish habitat in streams: transect spacing, sample size, and a proposed framework. N. Am. J. Fish. Manag. **14**: 607–615.

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A model of aquaculture biodeposition for multiple estuaries and field validation at blue mussel (*Mytilus edulis*) culture sites in eastern Canada

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Abstract: Development of mariculture in Canadian waters has outpaced the ability of regulators to adequately assess environmental impacts and coexistence with other resource users. In eastern Canada, suspended longline culture of blue mussels (*Mytilus edulis*) leads to depletion of seston and subsequent biodeposition of feces and pseudofeces. Based on the need to evaluate aquaculture effects over multiple farms, a model was developed to compare the rate of mussel egestion with the scale of culture and tidal flushing of particulate waste from estuarine waters. Egestion was calculated using a bioenergetic submodel, and tidal flushing was determined with a tidal prism method. A short-term field program of particle sensing and sediment trapping was undertaken in Tracadie Bay and Savage Harbour (Prince Edward Island) to examine model assumptions and for validation. A finite element model was used to verify tidal prism calculations. Expressing model output as sedimentation rate, predicted biodeposition in Tracadie Bay was less than that estimated from field results but within the range of estuary-wide variation. In Savage Harbour, the egestion model overestimated biodeposition, likely because culture density on leased areas was sparse. A ranking of sites based on susceptibility to culture impacts was devised for multiple culture sites.

Résumé : Le développement de la mariculture dans les eaux canadiennes procède plus rapidement que la capacité des agences de réglementation à évaluer les impacts sur le milieu et les conséquences sur les autres utilisateurs de la ressource. Dans l'est du Canada, la culture de moules bleues (*Mytilus edulis*) sur filières en suspension entraîne l'épuisement du seston et la déposition subséquente de fèces et de pseudofèces. Étant donné la nécessité d'évaluer les effets de l'aquaculture sur les sites d'élevages multiples, nous avons mis au point un modèle qui compare le taux d'égestion des moules en fonction de l'échelle de la culture et de l'évacuation des déchets en particules par la marée dans les eaux estuariennes. L'égestion a été calculée à l'aide d'un sous-modèle bioénergétique et l'évacuation par une méthode de prisme de marée. Nous avons entrepris un court programme d'études de terrain d'enregistrement des particules et de trappage de sédiments dans la baie de Tracadie et à Savage Harbour (Île-du-Prince-Édouard) afin de vérifier les présuppositions du modèle et d'en faire la validation. Un modèle à éléments finis a servi à vérifier les calculs du prisme de marée. Lorsque les résultats de la modélisation sont exprimés en taux de sédimentation, la biodéposition prédite dans la baie de Tracadie est moins importante que celle estimée d'après les données de terrain, mais elle se situe dans la gamme de variation qui existe à l'échelle de l'estuaire. À Savage Harbour, le modèle d'égestion surestime la biodéposition, probablement parce que la densité de la mariculture est faible dans les zones sous bail. Nous avons mis au point un système de classement des sites en fonction de leur susceptibilité aux impacts de la mariculture applicable aux sites d'élevages multiples.

[Traduit par la Rédaction]

Introduction

Aquaculture of finfish and shellfish in marine inshore waters can produce environmental impacts of concern to the management of coastal resources. It is well documented that waste material from food and fecal deposits enriches local sediments, often causing lowered sediment redox potential and oxygen and a shift toward anaerobic benthic metabolism (Grant et al. 1995; Christensen et al. 2003). There has been much less attention paid to far-field- or ecosystem-level effects of aquaculture and the ability of the environment to assimilate this additional organic loading. It is expected that

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aquaculture would produce observable impacts in the vicinity of the culture, as would any husbandry activity. For example, agriculture produces monocultures of crops in farmed fields with an inevitable loss of phytal biodiversity. The use of highly localized habitat changes as a measure of culture impacts is thus inadequate because it offers little in the way of extrapolation to changes in the larger ecosystem. Moreover, documentation of impacts in terms of faunal changes, such as shifts to opportunistic benthic assemblages, is not quantitative in terms of mass fluxes and is confounded in many estuaries where such communities are a preexisting condition (Grant et al. 1995).

For suspended shellfish culture, a major concern is the consolidation of small particles into feces and feeding waste (pseudofeces), causing their sinking to the bottom (Grant et al. 1995). It must be emphasized that because mussels feed on natural seston, they do not add nutrients or particles to the ecosystem, but they do repackage particles (e.g., phytoplankton to feces) and regenerate nutrients (e.g., organic nitrogen to ammonium). A variety of studies have shown that cultured mussels tend to have a significant effect on the dynamics of particles and nutrients in marine ecosystems (Dame and Prins 1998).

In light of these processes, three environmental interactions may be defined for mussel culture. (*i*) Dense culture of mussels depletes the water of phytoplankton. This depletion removes particles used as food by zooplankton or benthic suspension feeders (clams, mussels, oysters) and alters food availability to these organisms as well as to the mussels. (*ii*) Dense mussel culture produces excess sedimentation to the bottom. This constitutes a source of organic loading, leading to hypoxic and sulfidic conditions in the sediment, potentially stressing benthic communities. (*iii*) Nutrient flux from mussel excretion and benthic regeneration of biodeposits accelerate the turnover of nitrogen, making it more available to phytoplankton.

From a modelling standpoint, particle depletion and production of feces and pseudofeces may be coupled as complementary bioenergetic aspects of mussel feeding. The translation of impacts from point source to the larger ecosystem occurs through advection and diffusion, which are dependent on tides, winds, and estuarine circulation. The degree of impact in a system is directly related to its ability to disperse culture wastes (Chamberlain et al. 2001).

In Canada, the need to assess environmental effects of suspended blue mussel (*Mytilus edulis*) culture in multiple estuaries arises in part from legislative requirements of the Canadian Environmental Assessment Agency (http://www.ceaa.gc.ca). An important application of CEAA legislation involves mussel culture in Prince Edward Island, which has been ongoing for approximately 20 years, with many available sites under cultivation. There is presently no mechanism to evaluate whether the extent of culture affects mussel growth and alters ecological conditions in the ecosystem. It is impractical to conduct a multiyear study of every estuary used for aquaculture, especially when the industry is still expanding. Simulation modelling provides an effective means to evaluate a variety of estuaries simultaneously and compare their susceptibility to culture impact. For many systems, there are insufficient data for full-scale ecosystem models. Moreover, the time involved for screening multiple estuaries is prohibitive. We have therefore attempted to create a simplified model of suspended mussel culture that balances production of feces and pseudofeces versus physical exchange and yields an equilibrium mass potentially available for biodeposition.

Following the simplified approach in the model, we undertook field studies as a means of assessing the utility and value of short-term field programs aimed at providing groundtruthing for model predictions. The field program focused on measurements of seston, chlorophyll, and tidal level using in situ instrumentation and sedimentation rate using sediment traps. These measurements were employed in association with the following objectives: (*i*) produce a simplified generic model of potential biodeposition impacts that can be applied to multiple estuaries with minimal dependence on local conditions, (*ii*) compare model predictions of physical exchange with more complex circulation modelling results, (*iii*) examine the results of a short-term field study as validation of model results, and (*iv*) determine if model predictions can be extrapolated to multiple estuaries.

Materials and methods

Modelling approach

The above environmental effects focus on mussels, but the estuarine ecosystem involves a complex array of physical, chemical, and biological factors that influence both particles and nutrients. Chief among these is tidal- and wind-based movement of water and its constituents. Owing to river inflow and exchanges with the outer coast, any accounting of culture effects must be assessed in the context of an open system. An ideal approach to mussel ecosystem effects would be to track the production, utilization, and transport of nutrients and particles leading to quantification of the footprint caused by longline culture (Panchang et al. 1997). Cromey et al. (2002) have developed DEPOMOD for this purpose, but detailed local current speeds are required as input, and only a local effect is mapped.

In the model described below, we examine the dynamics of particles with an approach that simplifies their fluxes while still providing a quantitative measure of culture impact. Namely, we avoid most of the mechanics of deposition to the sediments. In nature, waste particles such as feces may have several fates including removal by flushing, deposition, disaggregation, and decomposition. In coastal estuaries, deposition to the sediments is a function of depth, stratification, bottom type and roughness, and shear stress. Larger systems contain a wide range of variation in these variables, and modelling of resuspension and deposition over large scales is not a casual undertaking, especially for multiple estuaries. If we simplify these pathways by turning off deposition, then the fate of egested feces can be portrayed as the balance between production by shellfish and flushing by tides. Except under high flushing conditions, this abbreviated view would lead to an overabundance of particles in the water column, since the deposition pathway is truncated. Our model undertakes this calculation, recognizing that the resultant particle loads are not measurable values but more an accumulation that is catalogued for the purpose of budgeting. The model employs a system-wide approach as opposed to the location-specific data necessitated by ground-

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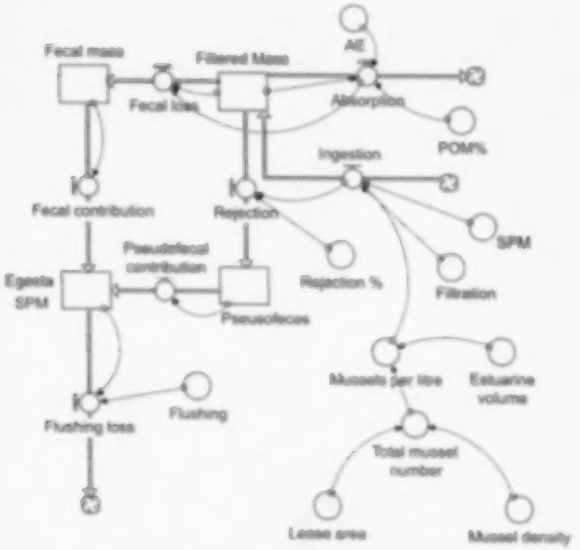
Fig. 1. Stella model of feeding and egestion by mussels and tidal exchange of total suspended particulate matter (SPM). AE, absorption efficiency of mussel digestion; POM%, percent organic matter of the seston. The boxes are standing stocks; large circles with arrows are fluxes; independent, smaller circles are rate coefficients and boundary conditions; and "clouds" represent terminal flows.



truthing, and there are implications for model validation as discussed below.

Based in Stella, a graphical model interface (ISEE Systems, Inc., Lebanon, New Hampshire; http://www.iseesystems.com), a mass balance is described between production of feces and pseudofeces derived from mussel bioenergetics and their flushing from the estuary (Fig. 1). We define egesta as the sum of feces and pseudofeces produced by the cultured mussels. If we first consider horizontal transport as their only fate, egesta accumulate until their rate of production is balanced by the rate of flushing, leading to a constant mass normalized to system volume and expressed as a concentration. This process may be described as an asymptotic function, where the maximum concentration effectively answers the question: if all mussel particle wastes are initially dispersed in the water column, what level of concentration would that produce in the estuary, given the rate at which they are flushed out? These egestion–flushing curves are analogous to those used to predict the balance of tracers in an estuary such as fresh water (Lowery 1998) or at a scallop aquaculture site to track particle advection (Grant and Bacher 2001). We reiterate that the accumulated egesta are a measure of throughput via mussel fecal waste and have units of concentration because they are normalized to volume; they are not an instantaneous concentration that can be observed in the field.

In systems with more mussels or lower flushing, this asymptote (equilibrium egesta) will be higher and require a longer time to reach a balance between production and flushing. The curves provide a way to incorporate the extent of culture, the size of an estuary, and its flushing characteristics into a single result; this is a minimal set of characteristics one would include in scaling culture to the size of a system. We distinguish the process of egestion from that of biodeposition, which we define as the rate at which egesta are deposited to the sediment surface. The two terms are related in that egesta are particulates potentially available for biodeposition. Calculation of biodeposition from egestion rate requires assumptions about the area over which egesta are deposited, an aspect that cannot be determined in a simple approach. In considering egesta as a suspended quantity, this source of uncertainty is avoided.

The assumptions of this model are as follows: (*i*) cultured mussels are homogeneously distributed in the estuary prescribed as the number of mussels calculated from a given farmed area, (*ii*) mussels are not food limited; there is an infinite far-field source of constant suspended particulate matter (SPM) for them to turn into egesta (seston depletion is considered separately), (*iii*) egesta are homogeneously mixed throughout the estuarine water column, i.e., there is no concentration gradient away from culture areas or near the bottom, and (*iv*) the ebbing tide removes egesta in proportion to water flux. The variables that change in application to other estuaries are estuarine volume, flushing rate, and mussel lease area (Fig. 1). Among these variables, only lease area is available from regulators or aquaculture organizations. Other data must be obtained from calculations using hydrographic charts or via field studies.

Mussel feeding and egestion

The processing of particles by mussels via feeding is modelled according the bioenergetic relationships detailed in Grant and Bacher (1998) and will be described only briefly here. Mussel feeding was simulated by estimating the volume of water filtered by mussels per day (filtration rate, litres per hour) (Fig. 1). Mussel ingestion was calculated as the product of filtration rate and ambient SPM to yield milligrams per hour. Material cleared from the water has two fates: rejection and ingestion. SPM rejected from the gills ends up as pseudofeces and is expelled from the mantle. Except in very turbid conditions, pseudofeces comprise the smaller portion of egestion compared with feces. Of the material entering the gut by ingestion, organic portions will be partially assimilated by the mussel and used in growth and respiration, while the entire inorganic component and nonassimilated organic matter will be expelled as feces. When SPM is mostly inorganic by weight, it is inevitable that most of the ingested SPM will become feces.

In the following culture scenario, mussels were considered to be harvestable adults (50- to 60-mm shell length) with a dry tissue (shell-free) weight of 700 mg. Mussels of this size are estimated to filter 56–96 L·individual^{-1}·day^{-1}, and their rate of assimilation feeding on natural seston was assumed to be 20% of particulate organic matter (POM) (Bayne et al. 1989; Grant and Bacher 1998; Cranford and Hill 1999). Pseudofeces production occurs via rejection of 10% of ingested material. In the model, ambient seston is critical because it drives mussel ingestion and determines the asymptotic value of cumulative egestion normalized to estuarine volume. Egestion–flushing curves were calculated for several levels of SPM to bracket reasonable values ob-

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Fig. 2. Site map of Prince Edward Island, eastern Canada, showing the location and bathymetry of Tracadie Bay and Savage Harbour. The general location of the mussel and reference sites is indicated. Each bay contains the finite element grid used in the circulation model. The tidally choked inlet mouths are not shown, but broken lines indicate the open ocean boundary of the model grid. In Tracadie Bay, Winter River is shown as the only sizeable source of fresh water in either system. The square in each estuary denotes the area in which mussel and reference sites were located. In total, mussel culture occupies 46% and 42% of the midtide area of the portions of the estuary shown for Tracadie and Savage, respectively.

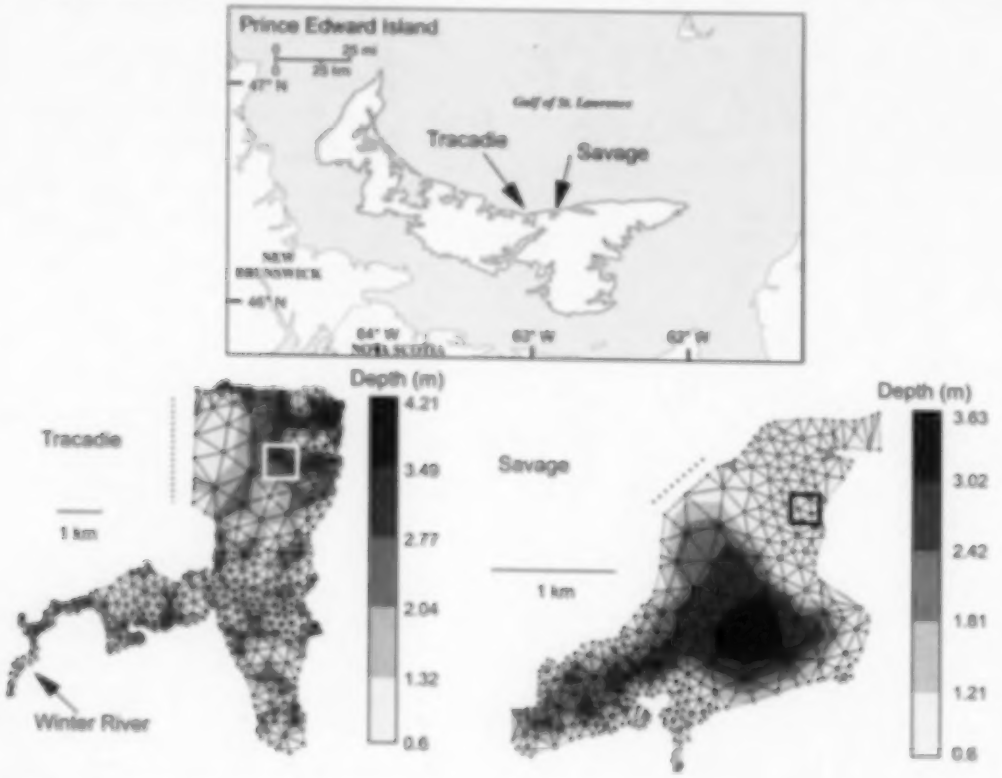

Table 1. Characteristics of mussel cultivation sites in field studies.

Estuary	Tidal range (m)	Total volume (m^3)	Tidal prism (m^3)	Cultured area (m^2)	Residence time (days)	Depletion index[a] I_D at 96 $L \cdot h^{-1}$	Depletion index[a] I_D at 56 $L \cdot h^{-1}$
Tracadie Bay	0.6	4.58×10^7	9.80×10^6	7.13×10^6	3.4	0.05	0.09
Savage Harbour	0.6	7.97×10^6	2.39×10^6	1.50×10^6	2.3	0.06	0.11

Note: Mussel cultivation area is total leased area; actual cultured area may be less.
[a]The depletion index is defined as the ratio of mussel clearance time to residence time as in eq. 2. Two values are given for different individual mussel filtration rates.

served at our study sites without including extremes of turbidity. Mussel density based on licensing data (see below) was calculated for the entire estuary and egesta were assumed to be distributed over the entire estuarine volume.

Seston depletion

Although the production of waste material provides one measure of impact, particle depletion is also an important effect as emphasized above. Since seston is mussel food, there is an intuitive aspect of seston depletion that makes it popular as a conceptual basis for gauging culture impact, despite the difficulty in documenting its magnitude. It is, however, one of the few calculations applied to bivalve culture that can be compared with biodeposition as a system-wide indicator of impact. The depletion model incorporates filtration and the volume of water processed by mussels compared with the tidal renewal of water available for suspension feeding. Following Dame (1996), clearance time (CT) (days) of the water column by mussels was defined as

$$(1) \qquad CT = V_T(NF_{ind})^{-1}$$

where V_T is total estuarine volume as in eq. 3 below, N is number of mussels in the estuary calculated as the product of average mussel density and lease area, and F_{ind} is individual filtration rate (cubic metres per day). Following Dame (1996), an index of seston depletion (I_D) was calculated as

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(2) $$I_D = CT(t_t)^{-1}$$

where t_t is flushing time based on the tidal prism from eq. 3 below. We discuss the differences between I_D and the egestion model calculations below.

Study sites

Two estuaries on the north shore of Prince Edward Island, Canada, were selected for modelling and field studies (Fig. 2; Table 1). Their proximity (12.5 km) allowed simultaneous field work at both locations. Tracadie Bay and Savage Harbour are similar in tidal range and inlet morphometry with barrier islands causing a tidally choked entrance and large deltaic features inside the mouth of the estuaries. Tracadie Bay is deeper and about six times the volume of Savage Harbour, with greater but still minor freshwater inflow via the Winter River (Table 1). However, the ratio of their tidal prisms (Tracadie–Savage) is only about 4, reflecting the shallower bathymetry of Savage that makes the tidally exchanged volume relatively larger compared with high tide volume. Tracadie thereby has a slightly longer residence time based on the tidal prism method (see below). Tracadie is also longer established as a mussel aquaculture site, with more absolute space for culture, but both estuaries have extensive areas designated for culture (Table 1). These barrier island estuaries represent only one type of culture site compared with rocky bays and other coastal systems of Atlantic Canada, but the approach is applicable to any tidal body.

Digital maps of both estuaries were created by digitizing their soundings and boundaries from which total and tidal volumes and surface areas for a given water level were calculated using Surfer (Golden Software, Golden, Colorado; http://www.goldensoftware.com). The areas of mussel leases for each estuary (D. Maynard, Department of Transportation and Public Works, P.O. Box 2000, 33 Riverside Drive, Charlottetown, PEI C1A 7N8, Canada, personal communication) were multiplied by the average density in longline culture (400 mussels·m^2 lease; Grant et al. 1993) to derive the total number of mussels in the system. This value was then divided by estuarine volume at mean high tide to derive the number of mussels per litre of water, diluting egestion over the entire estuarine volume (any tracer must eventually be diluted by high tide). The volume of mussel culture was calculated by multiplying culture area by an average sock length of 3 m.

Tidal exchange

Determination of tidal exchange is essential in the estimation of flushing of materials produced in the estuary. Flushing time (t_t), equivalent to residence time as defined by Dame (1996), was calculated with a refinement of the equation used by Gregory et al. (1993):

(3) $$t_t = -1\omega[\ln(V_T - V_P)/V_T)]^{-1}$$

where ω is the net time scale of a tidal cycle (hours), V_T is total estuarine volume, V_P is mean tidal prism volume, and $V_T - V_P$ is low tide volume, with all volumes in cubic metres. For semidiurnal tides, ω is consistent (e.g., ~12 h), but for mixed tides as in Tracadie and Savage, the smaller of the two daily peaks may not have the same volumetric replacement as the larger peak, so replacing the tidal prism may require >12 h. Using tide level curves (see below), the appropriate value for ω was calculated by summing the incremental volume replaced at each stage of flooding tide over several weeks and calculating the number of tidal volumes exchanged in that time. We have not included river input terms in Tracadie Bay because the Winter River has minimal discharge (Gregory et al. 1993) and acts more as a tidal slough than as a river. Flushing owing to river input can be included in the calculation made in eq. 3 by adding the discharge to the denominator (Strain and Yeats 1999). In addition, it is assumed that the tidal prism is thoroughly mixed with ambient water on every tide. For biodeposits, this assumption means that the proportion of mass flushed daily is identical to the proportion of tidal water flux (assumption *iv* above). Flushing times for both Tracadie and Savage calculated with this method are given in Table 1.

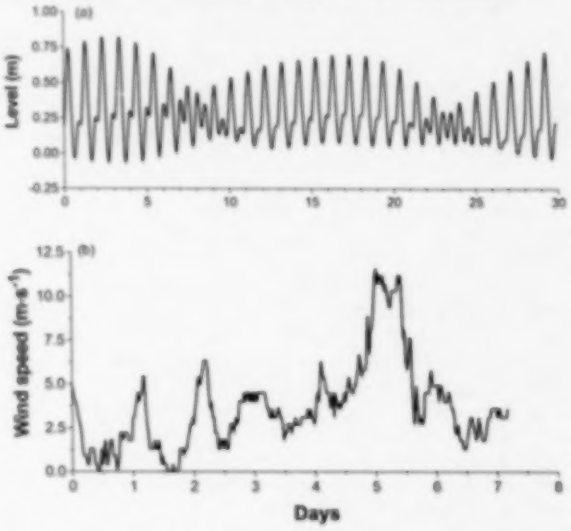

Fig. 3. (*a*) Tidal boundary conditions used in the finite element model of Tracadie Bay and Savage Harbour. These curves were generated from harmonic constituents as described in the text. (*b*) Wind records from Tracadie Bay over the study period.

Hydrodynamic model

The egestion model is firmly anchored in hydrodynamics and it is necessary to validate the tidal prism flushing estimates using a numerical model of circulation for Tracadie Bay and Savage Harbour (AquaDyn; HydroSoft Energie Inc., Montreal, Quebec; http://www.technum.com). This software generates a finite element mesh and incorporates a two-dimensional hydrodynamic model based on the St. Venant equations. It has previously been applied to estimate frictional effects in culture arrays of suspended scallops (Grant and Bacher 2001). The digitized boundaries and bathymetry for these two estuaries were imported into AquaDyn and used to generate a mesh of 445 and 325 nodes for Tracadie and Savage, respectively (Fig. 2). A tidal level curve used as a boundary condition was available for Savage Harbour from a database of tidal harmonics and was also applied to Tracadie Bay (Fig. 3). Owing to grid density and the

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proximity of reference and mussel sites (see below), we did not attempt to provide separate model output for the two sampling sites within each estuary. Instead, a single tidal curve and current record were generated for the local area of both Savage and Tracadie in which field sampling was undertaken. The tidal choking of both inlets causes a complex boundary condition for flow entry, requiring detailed and up-to-date bathymetry, which is likely different from that of the published hydrographic charts. To avoid this problem, we moved the open boundary for both inlets further inside the estuary (Fig. 2), so that the tidal boundary conditions were not dependent on entrance conditions. To evaluate tidal exchange in various parts of each estuary, we introduced a conservative model tracer value of 2 (arbitrary units) as a constant supply equally across the external boundary. Tidal transport was then applied to advect the material to the inside, where initial concentration was 1 unit. An inner node was considered at equilibrium when its concentration reached 95% (1.9) owing to this input. The curves are directly analogous to the egestion–flushing curves but are specific to various parts of the estuary, giving a two-dimensional spatial component to exchange.

To validate the results of the numerical model, we generated tidal level curves specific to the location of the tide gauges and compared with field values from these instruments (Wu et al. 1999). Tide gauge records were normalized to their means and fitted to M_2 (principal lunar, 12.42 h), K_1 (luni-solar, 23.93 h), and O_1 (principal lunar, 25.82 h) tidal harmonics based on initial examination of the data. A regression of the data was conducted with the following equation for M harmonic frequencies (f) (Emery and Thomson 1998):

$$(4) \qquad \sum_{q=1}^{M}\left[A_q \cos(2\pi f_q t_o) + B_q \sin(2\pi f_q t_o)\right]$$

where the coefficients A_q and B_q correspond to the amplitude (C_q) and phase lag (Φ_q) of harmonic q as follows:

$$(5) \qquad C_q = (A_q^2 + B_q^2)^{1/2}$$

$$(6) \qquad \Phi_q = \tan^{-1}(B_q/A_q)$$

Goodness of fit of the sea level time series via nonlinear regression using eq. 4 was used to assess how much of the tide gauge record was tidal in origin. Detided residuals were examined with respect to wind data from the weather station (see below).

Field studies

Field studies were conducted in July 2000, selecting a site adjacent to mussel longlines and a reference site. Choice of reference sites was dictated by the availability of culture-free areas between leases but close enough to mussel sites to have similar bathymetry and oceanographic conditions. In Tracadie, the reference site was 350 m from the mussel site, and in Savage, this distance was 100 m (Fig. 2). Both sites in Tracadie had a water depth of 4–5 m, while in Savage, depth was 3–4 m. Owing to the extent of mussel culture in both estuaries, the reference site was probably influenced by mussel culture, but it does not have the direct sedimentation of fecal matter from overlying longlines. Seston characteristics were documented to initialize the model and to assess the degree of heterogeneity between mussel and reference sites. A Seatech fluorometer (WET Labs, Philomath, Oregon; http://www.wetlabs.com) and optical backscatter sensor (D&A Instrument Company, Port Townsend, Washington; http://www.d-a-instruments.com) were deployed at the Tracadie reference site, while the adjacent mussel site had a Seatech fluorometer and transmissometer (10-cm path length) mooring. In Savage, the mussel site had a Seatech fluorometer mooring, while the reference site had a Seapoint fluorometer (Seapoint sensors, Inc., Exeter, New Hampshire; http://www.seapoint.com) and WET Labs transmissometer (25-cm path length). Tide–temperature gauges were deployed in both estuaries. Instruments were moored ~1 m off bottom by divers and sampling rate was set at 20- to 30-min intervals. A recording weather station (Davis Instruments, Hayward, California; http://www.davisnet.com) was mounted on a utility pole in Tracadie Bay to provide wind speed and direction.

Water samples were taken when moorings were deployed and retrieved and used for water quality analysis as well as instrument calibration. Duplicate 2-L samples were obtained 1 m above bottom using a Niskin bottle and three subsamples were filtered in the laboratory though prewashed and precombusted AMD GC filters (AMD Manufacturing Inc., Mississauga, Ontario; http://www.adventecmfs.com). SPM was measured after rinsing filters with a 3% ammonium formate solution and drying at 60 °C. Organic content was measured as filter weight loss on ashing at 450 °C. Chlorophyll was measured fluorometrically on separate filters following extraction in 90% acetone.

All instruments were calibrated simultaneously at the Bedford Institute of Oceanography in a flow-through raceway receiving natural, unfiltered seawater. Daily water samples were obtained surrounding a spring bloom period (71 days) in Bedford Basin and analyzed for chlorophyll and SPM as described above. The time of the water sample was matched to the instrument record for that day and used to construct linear regressions for each instrument. Values of r^2 for these regressions were >0.76 except for the optical backscatter sensor at the Tracadie reference site ($r^2 = 0.39$, $p < 0.0001$). For the Seatech fluorometer at the Savage mussel site, it was also necessary to apply a coefficient to scale the values to the observed range of field samples.

Sediment traps consisting of two replicate acrylic tubes with sealed bottoms (90-cm length, 12-cm inner diameter) were fixed to plastic crates mounted to patio stones and deployed by divers at each site. Trap lids were removed later by divers to avoid sedimentation arising from placement. Following retrieval after 6–7 days, trap contents were well mixed and subsamples taken to calculate total mass and analyze SPM, organic content, and chlorophyll as above.

To detect tidal patterns in the output of moored instruments, we performed spectral analysis by normalizing the signal to the mean and using a Hanning window. Siegel's test for confidence of peaks was used to examine the significance level of the spectrum ($\alpha = 0.05$).

Results

Egestion model

The cumulative mussel egesta (expressed as a concentration) compared with the ambient SPM concentration pro-

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Fig. 4. Results of the egestion model for Tracadie Bay and Savage Harbour. The three model curves are for different values of ambient suspended particulate matter imposed as a food source filtered by the mussels. (*a*) Tracadie Bay: dashed line, 1 mg·L^{-1}; dotted line, 2 mg·L^{-1}; solid line, 7 mg·L^{-1}. (*b*) Savage Harbour: dashed line, 1 mg·L^{-1}; dotted line, 2 mg·L^{-1}; solid line, 5 mg·L^{-1}.

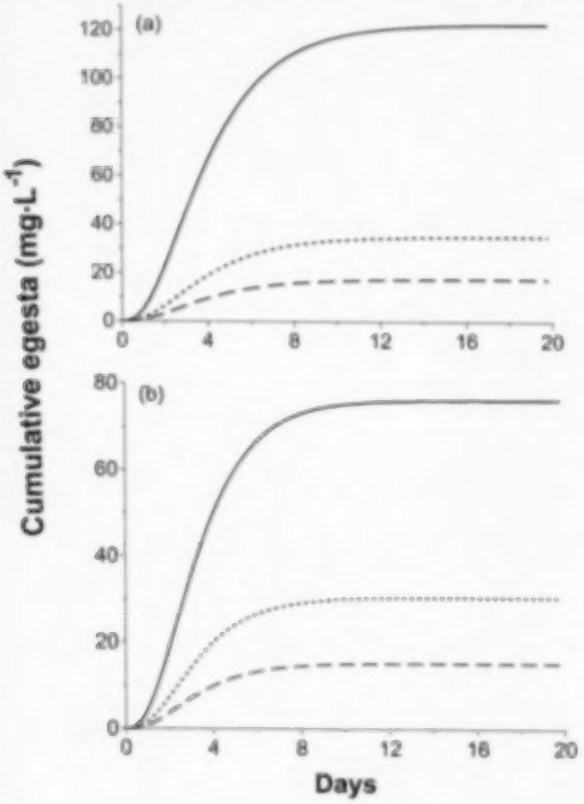
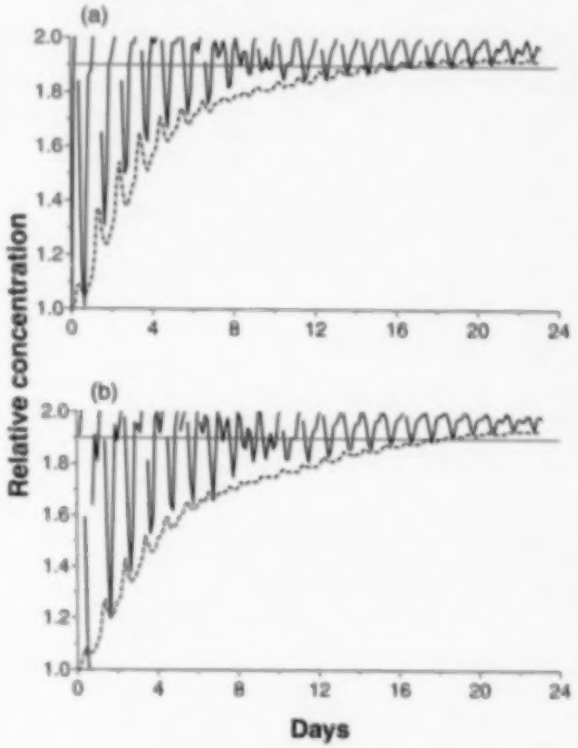


Fig. 5. Flushing curves generated for various nodes in both (*a*) Tracadie Bay and (*b*) Savage Harbour responding to the introduction of a tracer (2 arbitrary units) across the estuary mouth. The solid line refers to a node at the mouth of the estuary, and the broken line refers to a node at the mussel study sites shown on Fig. 1. The solid horizontal line in each plot is the 95% of maximum value.



vides an objective measure as to whether culture effects are detectable relative to background seston. Because the result is sensitive to absolute levels of SPM, three curves were presented for ambient SPM of 1, 2, and 7 mg·L^{-1} in Tracadie and 1, 2, and 5 mg·L^{-1} in Savage corresponding to the site-specific range of seston detected by the instruments. Using the flushing times in Table 1 for Tracadie Bay, the cumulative egesta for an ambient SPM of 7 mg·L^{-1} became asymptotic at a value of almost 122 mg·L^{-1} (Fig. 4*a*). This result means that for a constant ambient seston of 7 mg·L^{-1}, the cumulative mussel egestion of fecal material (prior to deposition) when in equilibrium with flushing and scaled over the whole estuarine volume will be equivalent to 122 mg·L^{-1}. The inference is not that the estuary becomes turbid (since the particles were filtered from the seston) but rather that the mass of potential biodeposits resulting from clearance of seston at 7 mg·L^{-1} will have this concentration when normalized to the size of the estuary. When the model was run with lower ambient SPM, the absolute value of the egesta plateau changed, since ingestion rate was less, but the egesta asymptote at ~14 times ambient SPM was maintained. The time at which equilibrium is achieved (95% asymptote) was 9 days.

In Savage Harbour, the results of the model demonstrated that the equilibrium egesta value was 76 mg·L^{-1} for the ambient SPM of 5 mg·L^{-1}. This equilibrium value, equivalent to 15 times ambient SPM, is relatively similar to that for Tracadie Bay but still an order of magnitude higher than ambient seston (Fig. 4*b*). The time to equilibrium (95% asymptote) was 7.6 days.

Circulation modelling

Mean current speed at the Tracadie mussel site (1.2 cm·s^{-1} ± 1.0 SD) was twice the magnitude that of the Savage mussel site (0.6 cm·s^{-1} ± 0.5 SD). We emphasize that these speeds are best considered relative values, since the truncated model entrances do not include the localized currents that might be specific to the complex channels in the inlet mouths. The results of the hydrodynamic forcing were used to examine the transport of conservative model tracers as a check on the cumulative egestion curves. The model experiment in which tracers were introduced at the mouth of the bay displayed strong tidal variations as tracers alternated between the lower and higher concentrations of incoming and

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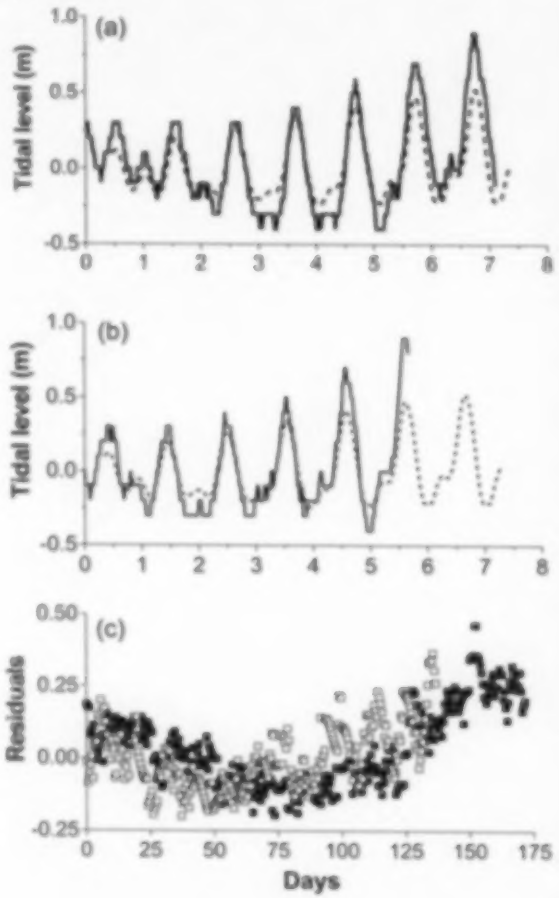
external water masses (Fig. 5). In both bays, hypothetical tracers in the mouths reached equilibrium concentrations in 8–9 days. At the mussel site in both bays, tidal variations in concentration were reduced compared with the mouth where enhanced flushing resulted in greater transits of water masses. The higher mean current speed in Tracadie yielded an equilibrium time (95% asymptote) of 16 days compared with 18 days (95% asymptote) for Savage (Fig. 5). The equilibrium times were greater than the 9 and 7.6 days calculated in the egestion model for Tracadie and Savage, respectively, based on the tidal prism (Fig. 4). Increased flushing rates are inevitable in the bulk calculations, since this e-folding method (i.e., e-folding time is the time that a species takes to have its concentration reduced to 1/e of its original value) assumes that the estuary is completely mixed and that particle exchange is simply a function of water exchange. The numerical model adds a more realistic spatial component in which interior estuary sites had reduced exchange rates (Fig. 5).

Tide gauge records for both Tracadie and Savage showed a mixed tide, with a steadily increasing amplitude during the study period (Figs. 6*a* and 6*b*). Harmonic regression indicated that the M_2, K_1, and O_1 tidal harmonics explained 77% and 83% of the variance in the time series for Tracadie (n = 343) and Savage (n = 273), respectively ($p < 0.001$ for both). We hypothesized that the residual variance in both cases would be correlated with wind speed, but this relationship was not significant. Owing to the high percentage of the variance explained by three tidal harmonics, we conclude that the tide gauge records reflect a tidal signal that was relatively uncontaminated by wind, changes in atmospheric pressure, and other influences. We note that the sea level recorded in the field includes the complex inlet bathymetry and its additional frictional effects on the tide, which are not incorporated into the model using a truncated inlet.

Model results for both estuaries showed mixed tides similar to those in the field data and general agreement in magnitude (Figs. 6*a* and 6*b*). The model underpredicted tidal levels at the end of the record. This portion of the observed record had the maximum residual variance relative to harmonic tidal prediction via eq. 3, indicating that nontidal effects on sea level only became important in the latter part of the pressure record (Fig. 6*c*). We thus conclude that the numerical model is validated with respect to reproducing sea level and volume exchange.

Fig. 6. Tide gauge and model data for mussel study sites. (*a*) Numerical model output of tidal level (broken line) compared with tide gauge records (solid line) in Tracadie Bay. (*b*) Numerical model output of tidal level (broken line) compared with tide gauge records (solid line) in Savage Harbour. (*c*) Residual variance in a harmonic regression (eq. 4) applied to the tide gauge records of Tracadie Bay (solid squares) and Savage Harbour (open squares).



Seston depletion

It is apparent that if mussel leases occupy a major portion of estuarine volume, and each mussel filters many times its ambient volume daily, then SPM will be depleted. This effect was quantified via the depletion index I_D, which compared mussel population filtration with flushing time owing to tides (Table 1). For an individual mussel filtration rate of 96 L·day^{-1}, mussel filtration of the estuary was 16–17 times more rapid than tidal renewal in Tracadie and Savage. At a lower filtration rate of 56 L·day^{-1}, this factor was reduced to 9–10. In both cases, filtration was substantially greater than the renewal of water, suggesting that food limitation is likely for both populations. This result is discussed below in terms of its implications for the egestion model assumptions and for mussel growth.

Field studies

Seston

Analysis of water samples from Tracadie Bay collected in July 2000 showed that SPM values ranged from 1 to 3 mg·L^{-1}. The moored backscatter sensor at the reference site displayed a generally increasing trend during the study with occasional spikes of up to 7 mg·L^{-1} (Fig. 7*a*). These spikes were not necessarily due to suspended sediment, since eelgrass and other detritus abundant in Tracadie Bay can also be detected by the sensors. The mussel site has a slightly increasing trend, but with generally lower values (<2 mg·L^{-1} except for days 2 and 3) than at the reference site. The weather station anemometry data from Tracadie Bay showed several wind events, with a general trend of increasing wind speeds to day 5 when winds of 12 m·s^{-1} were

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Fig. 7. Chlorophyll (broken line) and suspended particulate matter (SPM) (solid line) at the Tracadie Bay (*a*) reference site and (*b*) mussel site derived from moored transmissometer records and optical backscatter records, respectively, and moored fluorometers at both sites. Chlorophyll (broken line) and (or) SPM (solid line) at the Savage Harbour (*c*) reference site and (*d*) mussel site derived from moored transmissometer and (or) fluorometer records.

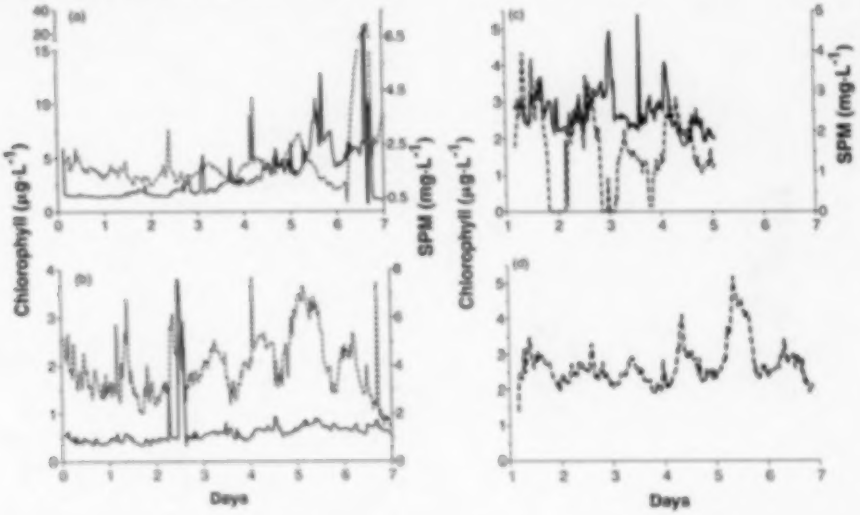
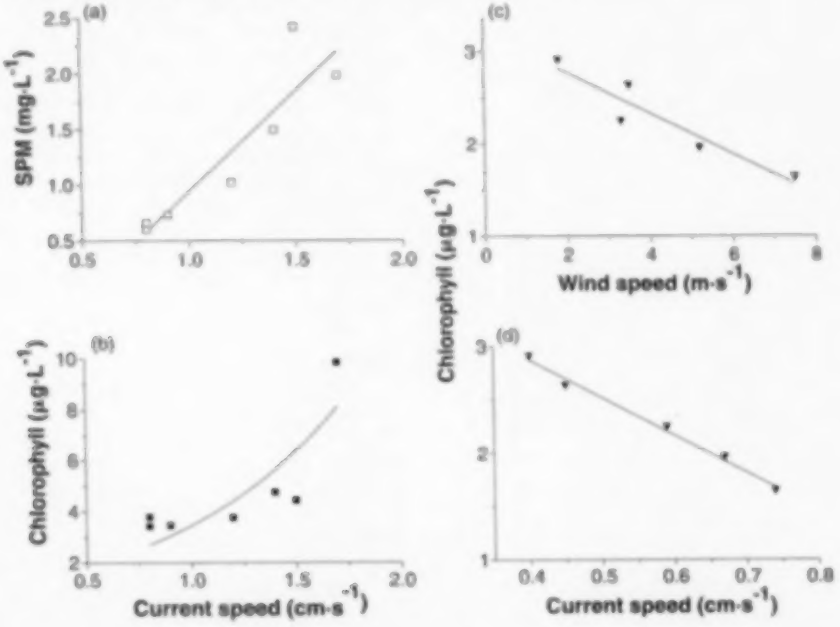


Fig. 8. Seston relationships with model current speed at the Tracadie Bay reference site: (*a*) suspended particulate matter (SPM) from optical backscatter sensor output, (*b*) chlorophyll from fluorometer output, and chlorophyll from fluorometer records at the Savage Harbour reference site in relation to (*c*) observed wind speed and (*d*) model current speed.



recorded (Fig. 3*b*). There was, however, no correlation between SPM and wind at either site. At the reference site, SPM was significantly correlated with current speed derived from model output (Fig. 8*a*), indicative of resuspension. While these low currents did not likely cause resuspension, they are proxies for critical currents elsewhere. No relationship occurred between SPM and current at the mussel site. Analysis of water samples from Tracadie Bay showed that organic content of SPM was high (~55%) and similar between mussel and reference sites (Fig. 9*a*).

Water samples from the Tracadie reference site displayed rather low chlorophyll values, often <1 μg·L^{-1} (Fig. 7*a*). Pig-

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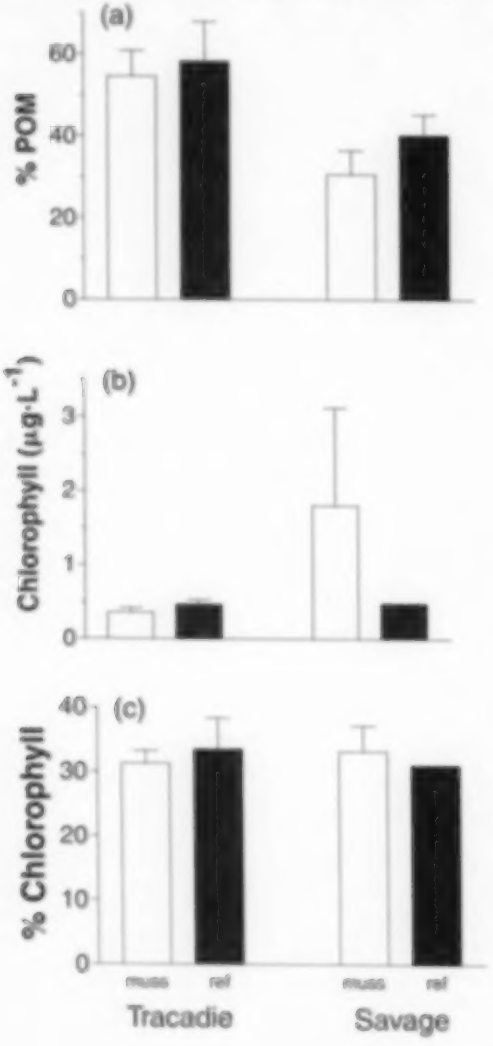
Fig. 9. Seston characteristics of samples from Tracadie Bay and Savage Harbour at mussel culture (muss) and reference sites (ref) in both estuaries. Values are mean + SE. (*a*) Percent particulate organic matter (POM) of total seston. Sample sizes for Tracadie mussel site and reference site and Savage mussel site and reference site are $n = 8$, 9, 5, and 7, respectively. (*b*) Chlorophyll concentration. (*c*) Percent chlorophyll of total pigments. Pigment sample sizes for Tracadie mussel site and reference site and Savage mussel and reference site are $n = 3$, 4, 2, and 1, respectively.



ments in SPM were 31%–33% chlorophyll, with no difference between reference and mussel sites (Fig. 9*c*). The temporal pattern of the fluorometer records was quite similar between the two Tracadie locations, with peaks lasting on the order of 1 day, but chlorophyll was slightly higher at the reference site (>3 µg·L^{-1}) (Fig. 7*a*) compared with the mussel site (usually <2 µg·L^{-1}) (Fig. 7*b*). Chlorophyll at the reference site displayed intermittently high values, especially later in the record, including chlorophylls up to 29 µg·L^{-1} (Fig. 7*a*). No significant tidal pattern in SPM was apparent from spectral analysis of either site, but a significant spectral peak occurred at 25 and 28 h at the mussel and reference site, respectively. Neither record was related to wind speed, but chlorophyll was exponentially related to modelled currents at the reference site (Fig. 8*b*). In addition, the highest chlorophyll value observed (days 5 and 6) came after the highest wind speed observed on day 5 (Figs. 3 and 7*a*). This result suggested tidal resuspension of benthic microalgae from bottom sediments.

Savage Harbour was characterized by ranges of SPM and chlorophyll similar to those of Tracadie (Fig. 7). The transmissometer and fluorometer at the Savage Harbour reference site indicated no apparent pattern (Fig. 7*c*). The absolute chlorophyll values cannot be compared via the fluorometers at the two Savage sites, since the mussel site instrument calibration is scaled to the range at the reference site. Significant spectral peaks in the fluorometer data occurred at 27 h (mussel site) and 28 h (reference site). The fluorometer record at the reference site had a strong negative correlation with both current speed and wind (Figs. 8*c* and 8*d*) but no relationship at the mussel site. This result is suggestive of flushing of phytoplankton from the estuary, but there is not a consistent trend in the fluorometer record to confirm this speculation.

Organic content of suspended material was similar between mussel and reference sites in Savage Harbour but on average substantially less than seston in Tracadie Bay (Fig. 9*a*). The percent chlorophyll of total photopigments was ~30% with little difference between mussel and reference sites and similar to that seen in Tracadie Bay (Fig. 9*c*).

Water column samples from both sites demonstrate an important facet of water quality as a measure of mussel impact on seston. There was no obvious difference in chlorophyll or SPM between mussel and reference sites. Where mussels are pervasive, their influence on seston depletion is system-wide and the depletion signal is present at both reference and mussel sites. Where mussel culture is less prevalent, a local depletion effect might be homogenized by mixing and not obvious from seston records. Moreover, an assumption of homogeneous SPM for the purpose of initiating the model appears to be valid based on comparison between mussel and reference sites.

Sediment traps

Sediment trap measurements from Tracadie Bay revealed that sedimentation rates near the mussel lines were about twice the values at the reference site (Fig. 10*a*). Organic content of trapped sediments was similar between reference and mussel sites but less than half that of SPM (Figs. 9*a* and 10*b*). Chlorophyll in sediment trap contents was slightly higher at the mussel site compared with the reference (Fig. 10*c*), indicating that the increased mass sedimentation rate at the mussel site produced even greater relative deposition of chlorophyll. In addition, the percent chlorophyll relative to total pigments was lower at the mussel site, suggesting more degraded particles sedimenting at the mussel site (Fig. 10*d*).

Sedimentation rates at the Savage Harbour mussel site were only slightly higher than at the reference site, and values were between those seen at the Tracadie Bay sites (Fig. 10*a*). Trap organic content and chlorophyll content

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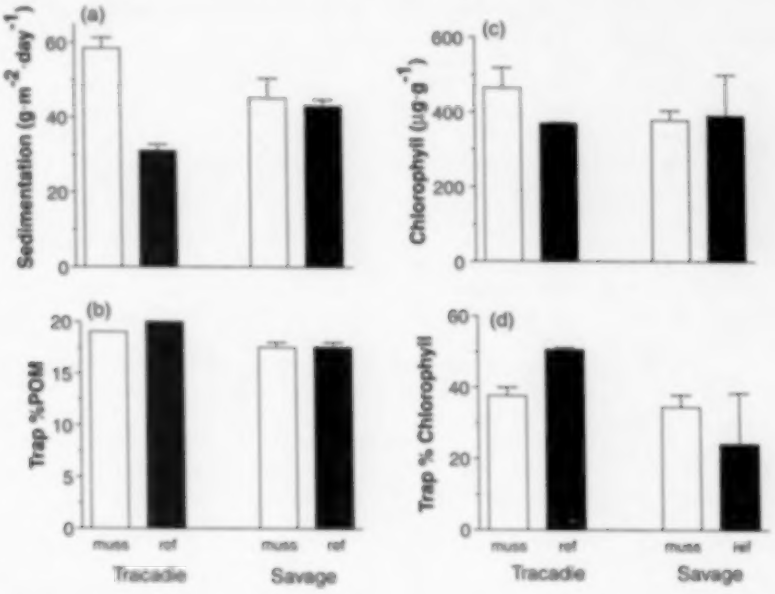
Fig. 10. Results of sediment trap studies in Tracadie Bay and Savage Harbour. Values are mean + SE; $n = 2$ traps for each value. (*a*) Mass fluxes; (*b*) percent particulate organic matter (POM); (*c*) chlorophyll concentration; (*d*) percent chlorophyll of total pigments. muss, mussel culture; ref, reference sites.



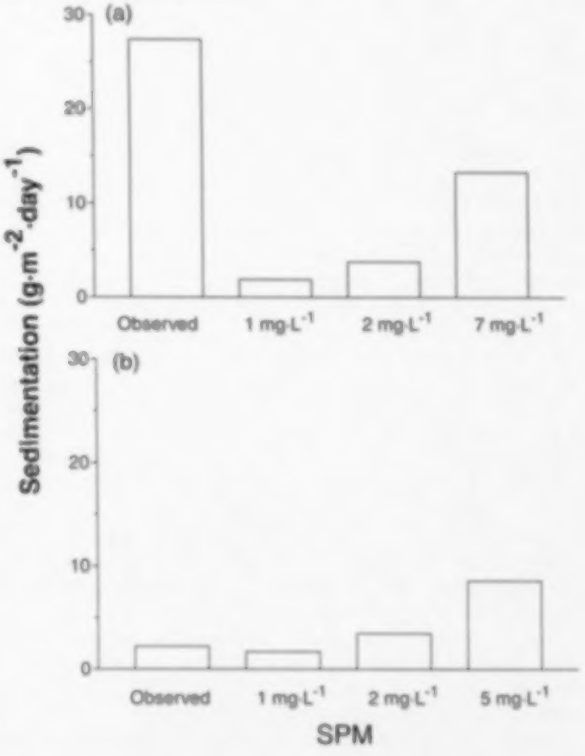
were identical between the two Savage sites and similar to values in Tracadie (Figs. 10*b* and 10*c*). The Savage mussel site had a somewhat higher percent chlorophyll in traps than the reference site, the opposite trend to that in Tracadie Bay (Fig. 10*d*).

Sediment traps thus demonstrate rather different results than found for seston in the water column, namely that there appear to be mussel–reference differences reflected in the quality and quantity of sedimented material. This is not unexpected, since sediment traps integrate longer-term patterns and effectively average the short-term variation that makes it difficult to gauge the local impact of mussels on the water column.

Model versus observed results

Field data from sediment traps was used for comparison with the results of the egestion model. We assumed that the difference between traps placed at mussel and reference sites was due to biodeposition from the mussel longlines (Grant et al. 1995). Sources of trap error arising from resuspension are accounted for in our calculations in that the background sedimentation (which includes resuspension) is removed when the reference site value is subtracted from the mussel site value. This difference as an estimate of daily biodeposition rate was compared with the egestion model run for 1 day. In this case, we set flushing in the model to zero to maximize model estimates as a worst-case scenario for potential biodeposition. Three values of predicted sedimentation were calculated corresponding to the range of SPM observed at the sites and input as food for the egestion calculations. This predicted egestion was distributed over the estuarine volume and deposited to the area of the estuary at midtide. The justification for these volume and area selections is discussed below.

Fig. 11. Modelled daily biodeposition for (*a*) Tracadie Bay and (*b*) Savage Harbour in terms of three different ambient seston concentrations and observed daily deposition at each site. SPM, suspended particulate matter.



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For Tracadie Bay, the observed sedimentation rate attributed to biodeposition was about twice that predicted for an ambient SPM of 7 mg·L^{-1} (Fig. 11*a*). Because the model prediction is averaged over the whole estuary, it should be less than rates determined in the midst of a mussel farm. In addition, empirical trap results used to estimate biodeposition reflect filtration of a variable ambient SPM and should thus occupy a range of predicted sedimentation rates (Fig. 11). Despite allowing for a range of SPM, predicted biodeposition provides only a conservative estimate of observed rate. However, as we discuss below, characterization of estuary-wide sedimentation rates with sediment traps at a single location is risky.

The results for Savage Harbour indicate that for low ambient SPM concentrations, the model provides estimates of biodeposition similar to those based on field measurements (Fig. 11*b*). At higher seston concentrations (5 mg·L^{-1}), model estimates of biodeposition overestimate the field values by a factor of 4. In Savage, the observed sedimentation attributed to mussels is low, since there was only a slight increase in trapped mass at the mussel site compared with the reference site (Fig. 11*b*). Anecdotal information from the site suggests that this low mussel signal is due to the fact that culture was sparser than indicated by the designated lease area. In this case, model estimates with their assumption of fully cultured leases lead to an overestimate of the potential biodeposition effects.

Discussion

Egestion model as an assessment tool

Our approach provides an objective way to evaluate the most important potential effects of suspended bivalve culture: biodeposition and seston depletion. It is essential to recognize that the SPM levels calculated in the egesta curves are not measures of turbidity caused by mussels but of cumulative fecal and pseudofecal output balanced against flushing. The fecal material is expressed as a mass concentration to provide a scaling of the egestion compared with the size of the estuary. We have chosen a default scaling factor, which maintains the simplicity of the approach (i.e., total estuarine volume (high tide)), since this dilution is inevitable with daily water exchange. This approach cannot be extrapolated to the effects of individual mussel leases on each other within an estuary because it is based on bulk exchange processes. The latter problem requires circulation models for each bay and spatially specific flushing curves.

The egestion model is similar to previous efforts to model aquaculture impacts in tidal waters in that rate processes such as release of waste material are balanced against flushing. This approach has been applied to removal of seston by bivalve suspension feeders (Dame and Prins 1998). Among finfish models, our application to multiple sites parallels the approach of Gillibrand and Turrell (1997) who calculated the balance between ammonia release by cultured salmon and its removal by tidal flushing.

These models have rarely been applied to biodeposits from shellfish aquaculture. In a recent study of oyster culture in Japan, Hayakawa et al. (2001) used a bioenergetic model of oyster growth to predict biodeposition and then assumed that fecal wastes were only deposited to farm areas. In this case, egestion rate was calculated on the basis of culture area and there was no consideration of volume. The lower sedimentation rate observed in the field compared with the model was used as evidence that the deposition area was beyond that of the farm. In our study, both harbours contain extensive areas of culture that occupy most of the volume of the shallow bays. The difference between use of total bay volume versus some other scaling factor related to culture is minimal in bays that are filled with culture.

To assess egesta accumulation and make comparisons between estuaries, it is convenient to consider an infinite source of food particles from which to produce feces. This assumption is not unreasonable, since bivalves draw their food from a much wider area than the boundaries of the farm. Natural mussel beds utilize food supplies from an area 11- to 16-fold greater than the beds (Smaal and Haas 1997). Nonetheless, egestion calculations should be accompanied by estimation of I_D, which provides an index of how important seston depletion might be in a culture system.

Ideally, the modelling should establish objective criteria for judging impacts, especially with regard to regulatory decisions. The egestion model establishes these criteria in relation to ambient seston levels. Based on our application of the model to mussel farms in Atlantic Canada, we propose the following classifications of the probability that egestion effects (observed in the field as biodeposition) could be detected in estuaries: case 1, cumulative egesta less than or equal to ambient SPM; case 2, cumulative egesta is 1–10 times ambient SPM; case 3, cumulative egesta is an order of magnitude or more than ambient SPM. In this scheme, ambient SPM is that imposed by the model. Used in a relative sense to categorize impacts according to the above criteria, knowledge of local seston is not essential, since the ratio of egesta to ambient SPM at the model asymptote is not sensitive to the absolute value of ambient SPM. Based on the criteria for classification of impact, model results suggest that both Tracadie and Savage would be classified as case 3. In the case of Savage, this rating is not supported by field measurements (see below).

Seston depletion

Seston depletion calculations agree with the scaling of the egestion model in that the impact of mussels on seston is not subtle. Previous calculations of seston depletion based on the depletion index (Dame and Prins 1998) indicate that values determined for Tracadie and Savage are lower than values for suspended mussel culture in France and Spain but similar to those of bottom mussel culture in the Dutch Oosterschelde. Meeuwig et al. (1998) suggested that chlorophyll in Prince Edward Island estuaries showed a deficit relative to levels predicted from available nutrients and accounted for this deficit by turbidity (light limitation) and mussel grazing.

Conceptually, it may be difficult to reconcile two measures of mussel impact where one removes seston (seston depletion) and the other examines accumulation of egestion. These indices are entirely consistent in the context of mussel bioenergetics, since depletion gauges removal of particles into the mussel and egestion quantifies fecal production from that food. It is essential to reiterate that our use of egestion as a suspended concentration is only a practical

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construct to simplify the particulate budget; it is not the appearance of particles measurable as a suspended mass.

Uncertainty, sensitivity, and groundtruthing

The sources of variation in the modelling approach arise from parameterization of physical exchange, seston, mussel bioenergetics, and cultured mussel biomass. In terms of physical exchange, the calculation using a tidal prism method provides at least a bulk measurement of water turnover, while the finite element model documents the extent to which there is spatial variation in flushing. The sensitivity to of the model to variable SPM is an important consideration in application to multiple sites with limited data. Our results indicate that the ratio of asymptotic egesta SPM to ambient SPM remains constant, important in defining the criteria of cases 1, 2, and 3 discussed above. The constant value of filtration rate that we employ in the model is reasonable compared with previous modelling and empirical studies of feeding in *M. edulis* (Prins et al. 1996; Grant and Bacher 1998; Cranford and Hill 1999). Moreover, Prins et al. (1996) showed in flume tunnel studies with intertidal mussel beds that individual clearance rates determined in laboratory measurements can be scaled up to population rates.

We chose fairly conservative default conditions for seston organic content (20%) and mussel absorption efficiency (20%). The effects of these low values is to route more mass flux through egestion and less through mussel tissue, with some potential to overestimate biodeposition. Subsequent field samples showed that percent POM of our sample sites ranged from approximately 30% to 60%. Cranford and Hill (1999) measured absorption efficiency in *M. edulis* in Nova Scotia and found an asymptotic relationship with percent POM. On this basis, at the range of organic content found at our study sites, absorption efficiency would range from ~20% to 70%. This source of variation is not problematic, since the egestion model is not very sensitive to either organic content or absorption efficiency. Their product multiplied by ingestion yields absorption to mussels, and unless percent POM and absorption efficiency are both very high, the majority of mass filtered by mussels is egested. Because the model is meant to be generically applied to multiple estuaries, we did not alter its default conditions based on the field studies at specific locations.

The estimation of sedimentation rates is not a fundamental aspect of the model we present. We employ the sedimentation calculation herein because it serves as one type of groundtruthing via sediment trap studies, although the latter are problematic in separating biodeposition from background deposition and in isolating the effect of resuspension typical in shallow habitats. It must be recognized that model output is specific to a fixed value for ambient seston, whereas the contents of sediment traps reflect biodeposition from mussels exposed to a variable range of seston concentrations. In addition, the strength of the biodeposition signal depends on cultured mussel biomass, demonstrated for Savage Harbour where the difference in sedimentation between the mussel site and reference site was relatively small, likely owing to the sparse culture in this estuary.

Our estimate of biodeposition from the model assumes that the influence of mussels is homogenized throughout the whole bay. In Tracadie, the mussels are so pervasive that this assumption is reasonable. In the field, we observe a difference between sedimentation rates directly beneath the mussel lines and those at the reference site, although it is likely that the reference site also receives input from biodeposition. In a scenario of dense culture, even a spatially averaged model estimate will not completely dilute predicted biodeposition. In an estuary with little mussel culture, the model estimate of biodeposition would be attenuated through the whole system. Under these circumstances, highly local sediment trap measurements beneath mussel culture would not serve as adequate validation data. However, in this case, the diluted model sedimentation rate would likely be similar to reference sediment trap measurements indicating the minimal impact of egestion when culture area is small compared with the size of the estuary.

Beyond these concerns, it is problematic to characterize sedimentation rate in an estuary with a single site. Our studies in Tracadie Bay subsequent to the present field measurements (J. Grant, unpublished data) indicate that the mussel station sampled here has the highest sedimentation rates in the estuary and that the range of spatial variation in Tracadie Bay is a factor of 4. For Tracadie, the discrepancy between modelled and field results is thus within the range of variation expected over the estuary. The implication of this result is not that the model is validated but rather that groundtruthing via sediment trap measurements is not definitive owing to the many sources of variation in the field results. We suggest that sediment traps are useful in validating model results if used judiciously in terms of location and if some information on their spatial variation is in hand.

Insights from field studies

Even a short-term field campaign was useful in assessing seston quality and quantity, especially using moored instruments. Beyond the sediment trap data, there are some indications that mussel feeding and egestion alter composition of seston in Tracadie Bay. The percent chlorophyll in seston pigments was not obviously different from that in the sediment trap contents, but material sedimenting from the water column was much lower in organic content than suspended particulates. This likely occurs because higher inorganic content is associated with denser particles (e.g., resuspended sediment) that preferentially sink relative to less dense suspended organic matter. It may also reflect the presence of biodeposits that are pelletized and depleted of organic matter.

The short-term field study provided valuable insights into the functioning of the two ecosystems, especially in regard to the relationship between wind–current and seston. Previous coastal studies have shown a correlation between wind and (or) current speed and seston or chlorophyll owing to the resuspension of sediments and benthic microalgae, respectively (Van Raaphorst et al. 1998). Field studies such as Grant et al. (1990) indicate the role of resuspension in supplying benthic microalgae or settled phytoplankton to cultured bivalves. We observed extensive cyanobacterial mats in sediment samples from the Tracadie mussel site, and ongoing studies of erosion thresholds at this location will aid in elucidating sediment resuspension in Tracadie Bay.

The negative relationships between seston and wind–current found at the Savage reference site were the opposite

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of those observed in Tracadie. We suggest that the Savage wind–current relationships reflect removal resulting from flushing (Monbet 1992). The fluorometer records at all sites displayed 25- to 28-h periodicity even in Tracadie (see also Dowd et al. 2002), possibly attributable to the higher of the daily mixed tidal peaks. Savage Harbour is characterized by a larger tidal prism relative to its volume than Tracadie. Tidal exchange is known to control chlorophyll at mussel culture sites in Nova Scotia (Grant et al. 1993) and in other estuaries (Muylaert and Raine 1999).

In conclusion, we are left with the following question: is the egestion model useful for predicting impacts of mussel aquaculture in multiple estuaries? In Tracadie Bay, the agreement of field results with a simple model is reasonable considering the variation inherent in the biodeposition calculation and in the interpretation of sediment trap results. Although the model can be used to make relative comparisons between estuaries in its present format, input of ambient SPM levels is helpful for comparison with field estimates of biodeposition. In addition, accurate knowledge of mussel culture density and longline spacing is obviously critical for model input as suggested for the Savage Harbour results. The tidal prism model of exchange is based on average values over whole the estuary, but it is clear that the flushing rate of most interior culture sites will be less than the bulk value. More detailed modelling such as the finite element model used here can provide exchange values for inner sites.

The conceptual basis of the egestion model is not diminished by lack of a definitive validation scheme, and it remains valuable as a screening tool for relative ranking of different estuarine systems. The comments of Gillibrand and Turrell (1997, p. 43) provide a concise summary: "However it should be emphasised that these models are used only to highlight problematic areas. When the models predict excessive impacts on water quality, further assessments are made, more advanced modelling may be carried out and monitoring of the site may be recommended. Thus, licenses are not refused solely on the basis of results from these models". If a site requires further study, examination of impacts at a smaller and more detailed spatial scale using a tool such as DEPOMOD (Cromey et al. 2002) would be a logical next step. In addition, further efforts might include comparison with other impacts (nitrogen cycling) as well as with other habitat indices (e.g., benthic enrichment index; Hargrave 1994) and even community-based measures of ecosystem health (Deegan et al. 1997).

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Costs and benefits of *Daphnia* defense against *Chaoborus* in nature

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Abstract: To estimate costs and benefits of antipredator defenses in the *Chaoborus–Daphnia* system, we employed lake enclosures wherein controls (C) had no predators, the predation (P) treatment had freely swimming *Chaoborus*, and the kairomone (K) treatment predators were sequestered in a mesh tube apart from the *Daphnia*. Population growth (r) of two *Daphnia pulex* clones, one responsive (RC) and the other nonresponsive (NRC) to *Chaoborus* kairomone, was estimated for each predator treatment. Cost of defense was calculated as $r_{(C,RC)} - r_{(K,RC)}$. Benefit was calculated as $r_{(P,RC)} - r_{(P,NRC)}$. Antipredator defenses of *Daphnia* towards *Chaoborus* kairomone led to a 32% reduction in population growth in nature. The benefit of the defense, however, was a short-term 68% enhanced population growth by a responsive over a nonresponsive clone in the presence of the actual predation threat. The benefit of the defense exceeded the cost, but cost was nevertheless substantial. Our results verify that the in situ effects of *Chaoborus* on *Daphnia* involve direct and indirect impacts.

Résumé : Afin d'évaluer les coûts et les bénéfices des défenses contre les prédateurs dans le système *Chaoborus–Daphnia*, nous avons utilisé une série d'enclos lacustres: les enclos témoins (C) ne contenaient aucun prédateur, les enclos de prédation (P) avaient des *Chaoborus* en nage libre et les enclos de kairomone (K) contenaient des *Chaoborus* enfermés dans des tubes de grillage séparément des *Daphnia*. Nous avons mesuré la croissance de la population (r) chez deux clones de *Daphnia pulex*, l'un (RC) sensible et l'autre insensible (NRC) à la kairomone de *Chaoborus*. Les coûts de la défense sont représentés par $r_{(C,RC)} - r_{(K,RC)}$ et les bénéfices par $r_{(P,RC)} - r_{(P,NRC)}$. Les défenses contre les prédateurs de *Daphnia* en réaction à la kairomone de *Chaoborus* entraînent une réduction de 32 % de la croissance de la population en nature. Les bénéfices de la défense sont, par ailleurs, une croissance additionnelle à court terme de la population de l'ordre de 68 % chez le clone sensible, par rapport au clone insensible, en présence d'une menace réelle de prédation. Les bénéfices de la défense dépassent les coûts, bien que ces derniers soient importants. Nos résultats confirment que les effets in situ de *Chaoborus* sur *Daphnia* impliquent des impacts directs et indirects.

[Traduit par la Rédaction]

Introduction

Our concept of the processes that shape food webs is typically focused on direct predator consumption of prey (e.g., Carpenter et al. 1985; McQueen et al. 1989; Ramcharan et al. 2001) and not on the indirect and ancillary costs of predation to prey populations. In some cases, this neglect is due to a lack of estimates of these ancillary costs in nature. A good example is the *Chaoborus–Daphnia* predator–prey system. Although this system is very well studied, plays an important role in lake food webs, and the antipredator defenses of the prey against the predator are well known, the costs and benefits of the defenses have not been estimated in nature, until now.

In the pelagic of lakes and ponds, *Daphnia* populations suffer heavy losses to predation by the invertebrate predator *Chaoborus* (Kajak and Rybak 1979; Hanazato 1990; Liljendahl-Nurminen et al. 2003) and employ a variety of defenses against this predator. The defenses include changes in life history, the growth of protective spines, and the adoption of antipredator behavior. Life history changes involve a shift towards larger sized individuals at first reproduction and production of fewer but bigger offspring (Spitze 1992; Weber and Declerck 1997; Riessen 1999). This defense is effective, as *Chaoborus* are mouth-gape limited and preferably prey on smaller individuals (Pastorok 1981). Protective spines on the dorsal lower margin of the head (neck spines) of juvenile instars have been shown to increase escape rate from *Chaoborus* attacks by up to 60% (Krueger and Dodson 1981; Parejko 1991; Repka et al. 1995). The antipredator behavior seems designed to reduce spatial overlap between the prey and predator. Since *Chaoborus* usually remains deep,

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in darker water during the daytime (Tjossem 1990; Voss and Mumm 1999), *Daphnia* avoid this predator by migrating upwards (Dodson 1988; Ramcharan et al. 1992). The effectiveness of this defense in unknown because of the practical difficulties involved in studying larger scale pelagic processes in the laboratory.

In nature, there are vertical gradients of temperature, oxygen, light, UV radiation, and food quality and quantity that can all have important effects on the vertical position of *Daphnia* in the water column (Davidson et al. 1998; Lampert et al. 2003; Winder et al. 2003). In fact, only recently has it been demonstrated that the behavioral defense of *Daphnia* against *Chaoborus* is anything but a laboratory phenomenon and actually occurs under near-natural conditions (Nesbitt et al. 1996). Since the behavioral defense against *Chaoborus* is inducible, the defense should entail a cost (Dodson 1974; Havel 1987; Schwartz 1991). Costs have been estimated for the morphological and life history defenses of *Daphnia* spp. to *Chaoborus*, at least in laboratory studies or theoretical models (reviewed by Tollrian and Dodson 1999), and were found to range from no costs to a 58% decrease in fitness. However, like the benefit, the costs of the behavioral defense against *Chaoborus* have never been included in food web models because these costs are difficult to estimate in the laboratory. As a result, although the *Chaoborus–Daphnia* system is an important trophic link in pelagic food webs and is also one of the best-known examples of inducible defenses, neither the benefits nor the costs of the combined defenses have ever been estimated.

Here, we estimate the costs incurred when *Daphnia* adopts behavioral and morphological defenses against *Chaoborus* and also the benefits of those defenses, all in terms of the intrinsic rate of population growth, r. Two aspects of the response of *Daphnia* to *Chaoborus* kairomone make our approach possible. Since the strength of antipredator behavior varies among clones, the benefit of the defense can be estimated as the difference in r between a protected and an unprotected clone when exposed to the predator. And since the defense is inducible for the protected clone, the cost of the defense can be estimated as the difference in r between population growth in controls and those exposed to just *Chaoborus* kairomone.

We conducted an enclosure experiment to estimate the effects of the various defense mechanisms in terms of costs and benefits in nature. We used two *Daphnia pulex* clones, one that could employ antipredator defenses against *Chaoborus* (responsive clone) and one that could not (nonresponsive clone). Three different treatments were conducted for each clone: predation (*Daphnia* together with the *Chaoborus* predators), kairomone (*Daphnia* were only exposed to predator kairomone), and control (*Daphnia* grew without any influence of predators). The difference in population growth between the control and kairomone treatment for the responsive clone should represent only the cost of the antipredator defenses, independent of the cost of predation (Table 1). When comparing population growth rates of the two clones in the predation treatments (normalized for the respective controls to account for clonal differences in life history parameters), the responsive clone is expected to have higher growth rates, which would be the benefit of the defenses (Table 1).

Table 1. Predicted growth rates of *Daphnia* clones according to different treatments and calculation of costs and benefits.

	Control	Kairomone	Predation
Responsive	*A*	*C*	*B*
Nonresponsive	*D*	*F*	*E*

Note: The responsive clone exhibits antipredator behavior. The nonresponsive clone does not exhibit antipredator behavior. *A*, *D*, and *F*, maximum population growth rate under given environmental conditions; *C*, growth rate affected by antipredator behavior; *B*, growth rate affected by both antipredator behavior and some predation; *E*, minimum growth rate, full predation pressure, no costs of defense. Costs of predation = $E - D$, costs of antipredator behavior = $A - C$, and benefits of antipredator behavior = $(B - E) - (A - D)$. To calculate costs and benefits as a percentage, both A and D = 100%.

Materials and methods

In a previous laboratory experiment, we evaluated 37 *D. pulex* clones, which were established as laboratory cultures by isolating individual females from 13 different water bodies, for their migration behavior, neck spine production, and life history responses (population growth rate r, neonate size, and size at first reproduction) in response to *Chaoborus* kairomone. Clones were determined to be genetically distinct by microsatellite analysis (Boeing 2002). Both clones used for the field experiment were collected in New York State, USA. One clone originated from a pond with a high density of *Chaoborus* predators but no fish, while the other clone came from Honeoye Fingerlake in which planktivorous fish are the main predators for *Daphnia*. The pond clone reacted strongly to *Chaoborus* kairomone by migrating upward in the water column, producing neck spines, and showing an increased population growth rate caused by earlier age at maturity as well as larger clutch sizes. This clone will hereafter be referred to as the responsive clone. The other clone did not show any response to *Chaoborus* and was designated the nonresponsive clone (Table 2). Among all the clones examined, the one isolated from Honeoye Fingerlake was one out of only three clones that did not respond to *Chaoborus* kairomone in the laboratory. We could not find two clones that differed fundamentally in their response to *Chaoborus* kairomone within one lake. The two clones were chosen based on their similarity in r, resistance to handling stress, and extremes of response and nonresponse to *Chaoborus* kairomone (Table 2) (Boeing 2002). Under ideal circumstances, multiple clones of each type would have been preferred. Unfortunately, we did not have the resources to run such an experiment in the field. Using multiple clones in the same enclosure bag would have created confounding competitive effects. Therefore, using only one clone for each type was the necessary trade-off to test our hypotheses. Both clones were grown to high densities in the laboratory before the beginning of the experiment.

Enclosure experiments

We estimated the costs and benefits of antipredator defenses toward *Chaoborus* under near-natural conditions with an enclosure study conducted during the summer of 1999.

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Table 2. Origin (pond or lake) and behavioral, morpholgical, and life history defenses of the responsive and nonresponsive *Daphnia* clones in laboratory evaluations.

	Responsive clone, pond				Nonresponsive clone, lake			
Laboratory trait	Control	Kairomone	*n*	*p*	Control	Kairomone	*n*	*p*
Depth selection behavior in 160-cm columns (cm below surface)	61.95±2.6	**9.23±3.8**	4	0.0008	46.19±6.6	52.84±6.4	3	0.18
Neck spine production of juvenile *Daphnia* (%)	3.64±1.5	**46.15±2.1**	5	<0.0001	0±0	0±0	5	—
Neonate size (μm)	0.574±0.004	0.574±0.009	5	0.99	0.590±0.006	0.608±0.010	5	0.07
Size at first reproduction (μm)	1.556±0.029	1.511±0.031	5	0.64	1.499±0.021	1.524±0.006	5	0.39
Clutch size (average third brood)	3.8±0.2	**1.3±3.1**	5	0.01	4.0±0.7	3.7±0.4	5	0.42
Population growth (*r*)	0.218±0.004	**0.260±0.003**	5	0.01	0.229±0.005	0.226±0.001	5	0.21

Note: Traits are listed as means ± 1 SE. Bold numbers indicate a significant difference from the control ($p < 0.05$), and *p* values were obtained with two-tailed Student's *t* tests. *n* is the sample size.

The treatments were the two *Daphnia* clones (responsive and nonresponsive) and three predator regimes (control, predation, and kairomone) in a factorial design with four replicates (24 enclosures in total). Enclosures consisted of transparent, non-UV-coated polyethylene, had a diameter of 1 m, and enclosed 7.5 m of the water column (5800 L). Each enclosure was suspended from a wooden frame, sealed at the bottom, and tied with a rope to a stabilizing anchor.

The enclosures were placed in Costello Lake (78°19′W, 45°36′N, Algonquin Park, Ontario, Canada). Costello Lake is a medium-sized (33.5 ha), oligotrophic (total phosphorus = 11.1 μg·L^{-1}), moderately brown-stained lake (dissolved organic carbon varies around 4 mg·L^{-1}, Secchi depth about 3 m) of circumneutral pH. High densities of *Chaoborus trivittatus* and *Chaoborus flavicans* as well as planktivorous fish are present throughout the summer (W.J. Boeing, personal observation). The zooplankton community is dominated by copepods but includes large cladocerans such as *Holopedium gibberum*, *Daphnia dubia*, *D. pulex*, *Daphnia dentifera*, and *Daphnia longiremis* (B. Wissel, unpublished data). Costello Lake represents an average lake for the region that was also secluded and human disturbance was minimal.

The enclosures were filled with lake water drawn from the upper metalimnion (2.5 m depth) to obtain intermediate nutrient, algae, and zooplankton values. The water was filtered through a 202-μm mesh, thereby removing large zooplankton such as *Daphnia* and *Chaoborus* while allowing the smaller natural zooplankton community to pass through. Afterwards, all enclosures were covered with screening (2-mm mesh) to prevent *Chaoborus* oviposition. Two days after filling, approximately 500 individuals from one or the other *Daphnia* clones were added to each of 24 randomly chosen enclosures. We conducted vertical hauls with a plankton net (30 cm in diameter, 130-μm mesh size) once a week to check *Daphnia* densities and on 3 July, after 14 days of growth, densities were adjusted to 1 individual·L^{-1} by removing extra *Daphnia* using plankton nets. A second, smaller tube (30 cm in diameter, 7 m long, and 495-L volume) made of 250-μm-mesh screening was then suspended in the middle of each enclosure. The mesh tube was used to sequester *Chaoborus* from *Daphnia* in the kairomone treatments while allowing free exchange of water, algae, and predator chemicals. On 4 July (day 1 of our experiment), *C. trivittatus* was added at a density of 1.1 individuals·L^{-1} to the randomly assigned predation treatments and the same total number of predators were placed in each of the mesh bags of the kairomone treatments. *Chaoborus* were caught the previous night from nearby Walker Lake with a 2-mm-mesh net. Costello Lake had high densities of *Holopedium* at that time that we could not keep out of the net and would have added undesired organic material to our enclosures. *Chaoborus* inside the mesh bags were fed with *Daphnia* that were removed from enclosures the previous day. No *Chaoborus* were put into the control. We chose *C. trivittatus* because it is the species in North America that remains in the planktonic stage throughout most the summer and is also a large species able to feed on even large *Daphnia* (e.g., Pastorok 1981). On 16 July (day 13) and again on 26 July (day 23), *Chaoborus* were added to densities of 1.2 individuals·L^{-1} and 0.9 individual·L^{-1}, respectively. This assured that, despite removal by sampling, predator density stayed above 0.7 individual·L^{-1}, a moderate natural density for *Chaoborus*.

We added moderate amounts of nutrients (10 μg P·L^{-1} as P_2O_5, 11 μg N·L^{-1} as NH_4 and $(NH_2)_2CO$, 9 μg K·L^{-1} as K_2O, 0.015 μg B·L^{-1}, 0.05 μg Cu·L^{-1}, 0.11 μg Fe·L^{-1}, 0.04 μg Mn·L^{-1}, 3.6×10^{-4} μg Mo·L^{-1}, and 0.04 μg Zn·L^{-1}) to each enclosure. The purpose was to maintain pelagic algae productivity by replacing lost nutrients due to algae sedimentation and eliminate food limitation as a confounding factor in *Daphnia* population growth.

Sampling

We sampled at 4-day intervals between 5 July (day 2) and 10 August (day 38). Zooplankton were collected with a closing net (30 cm in diameter, 130-μm mesh size) from four discrete depth intervals (0–1, 1–3, and 3–5 m and 5 m to the bottom) and were preserved in 4% sugar-saturated formaldehyde (Haney and Hall 1973). Temperature and oxygen profiles were taken at 1-m intervals with a probe (model 50B; YSI Incorporated, Yellow Springs, Ohio) lowered in the enclosures 1 day before collection of zooplankton samples.

We determined day–night distribution of zooplankton on days 10, 22, and 34. Daytime samples were typically taken around noon, while night sampling began 3 h after sunset.

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around midnight. Chlorophyll *a* was determined from 0.5-L samples pumped from 0–1, 1–3, and 3–7 m on days 6, 18, and 30 for three randomly selected enclosures per treatment. We could not sample all of the enclosures because of the time needed for processing. Water samples for chlorophyll *a* were kept in the dark and processed immediately upon return to the laboratory. We separated the algae into edible (<30 µm) and inedible (>30 µm) fractions with a Nitex mesh and filtered both fractions onto a GF/C filter (1.2-µm pore size). Filters were frozen at –20 °C for up to 3 months. Filters were then sonicated and chlorophyll *a* extracted in 100% acetone at 7 °C overnight. Chlorophyll *a* concentration was measured with a fluorometer (model 10-005R; Turner Designs Inc., Sunnyvale, California).

Sample enumeration and data analysis

Enumeration took place under a dissecting microscope (model MZ8, Leica Microsystems Inc., Bannockburn, Illinois) that allowed magnification up to 50-fold. *Daphnia* and *Chaoborus* were counted for each sampling date. To estimate population densities, we counted at least 100 *Daphnia* for each depth (0–1, 1–3, and 3–5 m and 5 m to the bottom) from each enclosure. If animal density was high, 10-mL subsamples were enumerated. *Daphnia* were distinguished by eye between adults (approximately >1.2 mm) and juveniles (approximately <1.2 mm). *Chaoborus* were counted as either first and second instar (<1 cm) or third and fourth instar (>1 cm).

Neck spine size of *Daphnia* was scored according to Tollrian (1993), where a morphologically normal neck was 0%, a little bump on the neck was 30%, and a bump with convex sides was 50% induction. Each separate spine accounted for an additional 10%.

Population growth (r) was estimated using the equation

$$r = [\ln(N_2) - \ln(N_1)]/\Delta t$$

where N_2 is the population density at time t_2 (later sampling date), N_1 is the population density at time t_1 (earlier sampling date), and Δt is the difference between time t_1 and time t_2 in days.

For easier comparison, population growth rates are expressed as a percentage. To adjust for life history differences between the clones, we normalized population growth values for the controls. Control treatments of both clones were set to 100% and the kairomone and predation treatments were determined relative to the control of the same clone.

Statistical analysis

On 6 July (day 3), 2 days after adding the *Chaoborus*, a storm destroyed some enclosures: two controls and one predation treatment for the responsive clone and one control for the nonresponsive clone. An unbalanced analytical design was the result of the loss of some replicates.

Statistical evaluation was conducted using SAS software (version 8; SAS Institute Inc., Cary, North Carolina). We used repeated-measures analysis of variance (ANOVA) with depth as the repeated variable to compare temperature and oxygen profiles among treatments. Variation in chlorophyll *a* among treatments was assessed with a three-way ANOVA using clones, predator treatment, and depth as independent variables. The effects of clone and predation regime on population growth rates, mean vertical distribution, and neck spine development were determined in separate analyses with two-way model III ANOVA (clones and predator treatments were fixed effects). The p values were adjusted with Tukey's test, normality was tested using Shapiro–Wilk's test, and homogeneity of variances was assured by Bartlett's test.

Results

Temperature and oxygen were consistent among treatments and the lake (repeated-measures ANOVA, $p > 0.05$). The epilimnion in both the lake and the enclosures was 3 m thick and temperature ranged between 20 and 25 °C. The temperature dropped quickly below 3 m and reached values around 7 °C at the bottom of the enclosures. Oxygen levels stayed between 6 and 8 mg·L^{-1}. The edible fraction of chlorophyll *a* (<30 µm) on day 6 was lower in the enclosures with the nonresponsive clone (20 µg·L^{-1}) than in those with the responsive clone (35 µg·L^{-1}) ($p = 0.001$).

Neck spine induction differed between the two clones in the field as it did in the laboratory. The responsive clone produced neck spines only in the kairomone (36.62% ± 1.43% induction) and predation (37.95% ± 4.28%) treatments, while the nonresponsive clone failed to do so in all treatments (two-way ANOVA, $p < 0.0001$).

Although in the laboratory, the population growth rate of the responsive clone in the kairomone treatment was higher than in the control owing to earlier maturation and larger brood sizes (Table 2), we could not confirm any differences in life history parameters in the field. We measured more than 120 *Daphnia* from each enclosure on day 10. There was no indication for increased body length of *Daphnia* owing to *Chaoborus* kairomone or predation treatment for either clone. We also did not find any evidence for a change in number of eggs per ovigerous female among treatments.

Vertical distribution during daytime was stable for all treatments in both clones for the first 14 days. Afterwards, the mean distribution dropped in all enclosures. Since the only night sample we have during that interval was on day 10, those are the data shown in the graph (Fig. 1). Predation regime had different effects on the vertical distribution of the two clones. Both clones preferred the epilimnion (0–3 m) during daytime (Fig. 1). However, only the responsive clone significantly decreased its mean vertical distribution by 1.11 m in response to predator kairomone (dashed lines in Fig. 1) (two-way ANOVA, $p = 0.0077$). In the predation treatment, the responsive clone was 1.17 m higher when compared with the control ($p = 0.0002$). *Chaoborus* mainly remained in the deepest sample layer (5–7 m) in all predation treatment enclosures. At night, both clones showed patterns of reverse migration and moved to deeper water layers. The responsive clone distributed itself evenly throughout the water column in the control. The *Daphnia* in the kairomone treatment remained on average 0.75 m and in the predation treatment 1.53 m higher than in the control. The nonresponsive clone stayed more clustered at intermediate depths. The distributions of control and kairomone treatments were almost identical, while in the predation treatment, nonresponsive *Daphnia* were virtually absent in the

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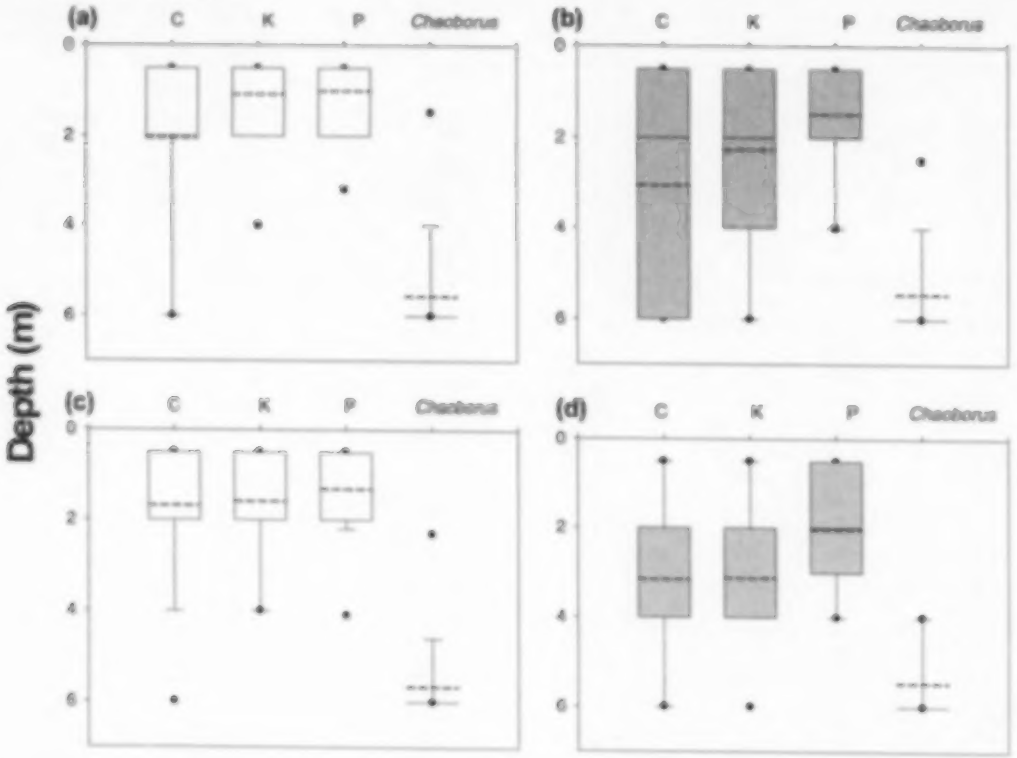
Fig. 1. Boxplots of vertical depth distribution of *Daphnia* and *Chaoborus* on day 10 during the day and night in the controls (C), kairomone treatments (K), and predation treatments (P) for the (*a* and *b*) responsive clone and (*c* and *d*) nonresponsive clone. The solid horizontal line is the median and the broken line is the mean. The box includes the second and third quartiles, and the deviation bars represent the 10th and 90th percentiles and the dots the 5th and 95th percentiles. Figures 1*a* and 1*c* are the day samples, and Figs. 1*b* and 1*d* are the night samples.



bottom of the enclosure bags, which led to a 1 m shallower distribution. *Chaoborus* showed no vertical migration pattern and remained at the bottom of the enclosures even at night.

On day 14, all treatments were at or past their peak of *Daphnia* population density. Therefore, we only present data for that time period, as this is relevant for the calculation of costs and benefits of *Daphnia* antipredator defense and density-dependent factors probably drive the declines of the populations. Population trajectories reveal that both clones had positive growth rates from day 0 to day 10 in the controls, after which the populations started to decrease (Fig. 2). For the responsive clone, population growth in the kairomone enclosures slowed for 9 days after addition of predators into the mesh bags. This caused a delay in the population peak of about 4 days. Similar to kairomone treatments, growth of the *Daphnia* population exposed to predation also slowed for 9 days after predator addition and peaked on day 14. The nonresponsive clone maintained higher overall densities than the responsive clone. Control and kairomone treatment of the nonresponsive clone did not differ from each other, and dynamics were comparable with the controls of the responsive clone. In the predation treatment, the nonresponsive clone showed a strong decrease shortly after predator addition and then grew to a maximum on day 14, 4 days after the control and kairomone enclosures had reached their maxima.

The time period of positive population growth (day 0 to day 10) of the control was used to calculate population growth rate for *Daphnia* in both the control and kairomone enclosures, and the differences in growth rates between different treatments were used to estimate the costs and benefits of defense between successive sampling dates (see Materials and methods) (Table 3). Both costs and benefits varied quite alot. Costs ranged from a low of −48.4%, indicating that *Daphnia* populations actually grew faster with predator kairomone, to a high of 153.3%, indicating a strong cost of prey defense. The value for cost of the defense calculated over the entire period from day 0 to day 10 was 32.3%. Although we did not observe a change in numbers of eggs per ovigerous female, by day 10, the percentage of adult females that were ovigerous was significantly lower in the kairomone and predation treatments of the responsive clone than in the control (two-way ANOVA, $p = 0.034$). Similarly, the benefit of the defense varied from a low of −146.8%, indicating that predation somehow benefited *Daphnia*, to a high value of 68.4%, indicating a strong advantage of the defense. This latter value was estimated from day 2 to day 6, the only period when *Daphnia* suffered clear losses to *Chaoborus* predation; thus, we believe that the value of

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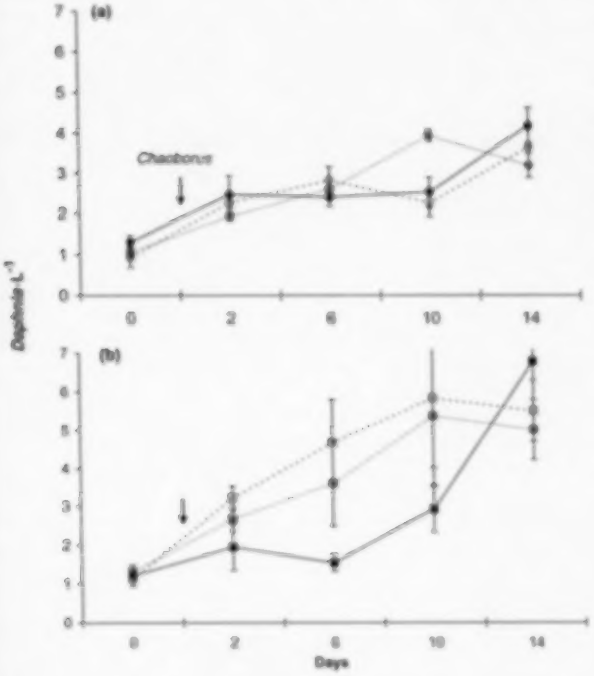
Fig. 2. Population dynamics (mean ± SE) of *Daphnia* clones between days 0 and 14. The arrows indicates *Chaoborus* addition on day 1. (*a*) Responsive clone; (*b*) nonresponsive clone. Shaded symbols, control; open symbols, kairomone; solid symbols, predation.



68.4% is the best estimate of the benefit of antipredator defenses.

Discussion

To summarize the results, the environmental conditions within the enclosures closely matched each other and the lake and were also well within the ranges of tolerance for both *Daphnia* and *Chaoborus*. Oxygen concentration was always above 6 mg·L^{-1}, which would not have been stressful for any of the species in our experiments (Davidson et al. 1998; Sell 1998). Besides *Daphnia*, there were also up to 20 *Bosmina*·L^{-1} and 2 copepods·L^{-1}, which could have served *Chaoborus* as prey. Levels of chlorophyll *a* were a little higher in the treatments with the nonresponsive than in those with the responsive clone.

In terms of antipredator responses, the field results matched our expectations based on the laboratory bioassay (Boeing 2002) fairly well. Neck spines were produced in the kairomone and predation treatments but only by the juveniles of the responsive clone. However, in response to either *Chaoborus* kairomone or real predation, there was no evidence in the clones of a life history response (increase or decrease in egg production or changes in body size). Estimates of population growth rate showed slightly higher values of *r* for the nonresponsive clone compared with the responsive clone. The two clones exhibited some differences in vertical distribution in the control enclosures. The nonresponsive clone had a tendency to stay up higher in the water column during the day and was not as evenly distributed as the responsive clone at night. The one unexpected result was that not just the responsive clone but also the nonresponsive one exhibited a reverse diurnal migration pattern, migrating down at night. However, as seen in the laboratory bioassays, only the responsive clone reacted to the kairomone treatment with a higher vertical position. In contrast, the nonresponsive clone had the same behavior in the kairomone treatment as in the controls. Including Nesbitt et al. (1996), this is now only the second time that the behavioral response to *Chaoborus* has been induced in nature. For the responsive clone, maintaining a high vertical position in the kairomone treatments relative to the controls during both day and night was a good defensive strategy, as *Chaoborus* remained at depth. In the predation enclosures, both clones remained highest in the water column among all of their treatments but, as with the kairomone treatments, the responsive clone again showed the stronger avoidance response (change in position relative to the controls). The absolute vertical position of the nonresponsive clone in the predation treatment was shallower than that of the control or kairomone treatment, which might have been due to predation losses to *Chaoborus* in deeper water layers rather than a behavioral response.

We found that defending against *Chaoborus* caused a reduction of 32.3% in *Daphnia* population growth, and we estimated the benefits to be 68.4% enhanced population growth, exceeding the costs by 36%. This was the first time that benefits for *Daphnia* antipredator defense were estimated and it was also the first time that costs were measured in nature and included the behavioral migration response. The reduction in population growth was probably due to the decreased percentage of ovigerous females in the kairomone treatments.

The calculation of the cost of antipredator defense was fairly straightforward, as the differences in population growth between control and kairomone enclosures were compared within the same clone (responsive). We estimated the cost of antipredator defenses to be a 32% reduction in population growth in the kairomone compared with the control treatments. The populations in the controls had a higher population growth rate and reached maximum population densities faster than those exposed to kairomone. The reduction of population growth in the kairomone treatment can only be explained by induced antipredator defenses.

Several different mechanisms could have accounted for the cost of the antipredator defense. We observed both neck spine production and upward migration in the responsive clone. The neck spine production itself probably did not contribute to lower population growth. This clone did not experience a reduced fertility rate owing to *Chaoborus* kairomone exposure in previous laboratory experiments in which neck spine production exceeded the induction observed in the field (Boeing 2002). However, the behavioral upward migration probably did cause the observed cost. According to traditional belief (Bottrell 1975; Stich and Lampert 1984), *Daphnia* in the kairomone treatments experienced warmer temperatures than in the control treatments, which should enhance population growth in the kairomone treatment by 10% compared with the control treatments

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Table 3. Population growth rates (r) of responsive and nonresponsive *Daphnia* clones for different time intervals and calculation of costs and benefits for different time intervals.

	Responsive clone r			Nonresponsive clone r				
Days	Control (n = 2)	Kairomone (n = 4)	Predation (n = 3)	Control (n = 3)	Kairomone (n = 4)	Predation (n = 4)	Costs (%)	Benefits (%)
0–2	0.30±0.02	0.45±0.06	0.32±0.02	0.35±0.04	0.43±0.02	0.23±0.01	–48.37	39.55
2–6	0.07±0.00	0.05±0.00	–0.01±0.00	0.07±0.01	0.09±0.01	–0.06±0.01	26.58	68.41
6–10	0.10±0.00	–0.06±0.01	0.01±0.00	0.1±0.01	0.06±0.01	0.16±0.01	153.27	–146.77
0–10	0.13±0.01	0.09±0.01	0.07±0.01	0.14±0.02	0.16±0.01	0.09±0.01	32.25	–11.78

Note: Values represent mean ± SE, and n is the sample size.

(considering that the average metalimnion temperature was 10 °C below the epilimnion temperature and 20% more *Daphnia* stayed below the thermocline in the controls than in the kairomone treatment). However, recent research is suggesting that temperature can have negative effects on large body sized *Daphnia* as energy becomes limiting (decreased assimilation – metabolism relationship) (Weetman and Atkinson 2004). Another likely cost is increased competition for food owing to crowding. As daphnids migrate upwards, they use a smaller volume of the water column and would compete more strongly for the available food. Steiner (2003) demonstrated that effects of competition can outweigh actual *Chaoborus* predation. Moreover, feeding rate may itself be reduced in the presence of *Chaoborus* kairomone (Ramcharan et al. 1992) or crowding chemical (Lurling et al. 2003), which may further reduce somatic growth rates. Although the number of eggs produced per ovigerous female was the same among treatments for the responsive clone, there was a significant decrease in the percentage of females producing eggs, which might be explained by competition or crowding. Ebert (1993) found a reduction in the number of eggs owing to food limitation in *Daphnia magna*, while Lynch (1989) and Boersma (1995) also observed reduction in egg size of *D. pulex* and *Daphnia galeata*, respectively. We did not measure egg size and could find no reference to reduction in the percentage of ovigerous females owing to resource limitation. Exposure to UV radiation might have also contributed to the cost of antipredator defense (Williamson 1996). Harmful radiation can penetrate down to about 1 m in lakes with a dissolved organic carbon content comparable with that of Costello Lake (Leech and Williamson 2000). Migrating upwards in the daytime as a response to *Chaoborus* kairomone may have negatively affected *Daphnia* survival and reproduction (Grad et al. 2001).

Our estimate of 32.3% reduction in r is a higher value for *Daphnia*'s defense against *Chaoborus* than has been estimated in the laboratory. Exposure to *Chaoborus* kairomone in the laboratory has had negative effects on *Daphnia* population growth that varied widely between 0% and 28% (Havel 1987; Riessen and Sprules 1990; Walls et al. 1991). The variation can be partly explained by differences among experiments in exposure time to predator kairomone (Riessen 1999) as well as genetic variance. However, all of these laboratory estimates could consider only morphological and life history costs. Only in nature could the cost of behavioral defenses be properly estimated, and in our study, it is likely that enhanced competition for food and exposure to UV radiation reduced *Daphnia* r more than the cost of the morphological and life history defenses.

We calculated the benefits of antipredator defense as the difference in predation impact (difference in r) between the responsive and nonresponsive clones. This approach is efficient but can be confounded by differences in r between the clones in the controls. In the laboratory bioassays, the two clones had similar r values. However, in the field, the nonresponsive clone had a higher r and reached a higher maximum density than the responsive clone. Also, slight differences in vertical distribution in the control treatments between the clones could potentially interfere with the results. As the estimate for the benefit was adjusted for differences in r of the controls, the effects of different population growth rates were minimized. The higher density of the nonresponsive clone was likely the reason why levels of chlorophyll *a* were reduced in the enclosures with this clone.

The behavior of the predator also affected our estimates of the benefits of the defense. *Chaoborus* failed to show a strong upward migration at night that is typically found in nature (Tjossem 1990; McQueen et al. 1999). This might be due to a shock response. Dawidowicz (1993) observed in his experiment that after introduction into 1-m experimental tubes, *Chaoborus* initially failed to migrate, and only after about 3 weeks did approximately 50% of the population rise to the epilimnion at night. Similarly, *Chaoborus* in other enclosure experiments showed only a very subtle upward migration during nighttime (Nesbitt et al. 1996; Young 2002; B. Wissel, unpublished data). Without upward migration, overlap between predator and prey would have been low, thereby reducing predation impact. Calculations of an overlap index (Williamson and Stoeckel 1990) between the responsive and nonresponsive clones in our experiment revealed negatively correlated prey and predator distributions in both clones during day and night. Certainly, a predator has to encounter its prey for predation to occur. In our experiments, we know only that on day 10, there was little overlap between *Chaoborus* and *Daphnia*, yet on previous days, there was a clear predation effect. It is possible that early in the experiment, the predator had a day–night vertical distribution that caused higher overlap with the prey. It is also possible that *Chaoborus* stayed in the lower water layers from the start to the end of the experiment but that this degree of overlap was sufficient to reduce prey numbers when prey populations were low. As the prey increased, *Chaoborus* could not show a numerical response, and the proportion of prey lost to predation would fall. The reduction in population growth rate between days 2 and 6 for both

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clones as well as the shallower distribution in the predation treatments can only be explained by actual predation on *Daphnia* by *Chaoborus*, which allowed us to estimate a benefit to *Daphnia*'s defense.

Our estimate of a 68% reduced mortality rate owing to antipredator defenses is higher than laboratory estimates for the benefits of other defenses. Neck spines alone increase escape rate from *Chaoborus* attacks by up to 60% (Krueger and Dodson 1981; Parejko 1991; Lüning 1995). The high estimate in our study might be due to a simultaneous benefit of behavioral and morphological defenses.

In summary, ours is the first attempt to measure the costs and benefits of *Daphnia*'s antipredator defenses against *Chaoborus* in nature. In this first approximation, we found a reduction in population growth of 32% owing to antipredator defenses, probably as a result of decreased energy efficiency of *Daphnia* owing to higher temperature exposure, detrimental effects of UV radiation, crowding, and competition for limited food resources in the upper water layer. The estimated benefits of the antipredator defenses of 68% outweigh the costs, as would be expected (Sih 1982; Dill and Fraser 1984; Kohler and McPeek 1989). Over the course of a growing season, with benefits exceeding costs by 36%, the advantage of an invulnerable over a vulnerable clone can be considerable, even if *Chaoborus* predation is limited to short periods of time. Although *Daphnia* are an ideal study organism to measure costs and benefits of inducible defenses, clonal variety is large and different combinations of behavioral, morphological, and life history defenses occur. Therefore, costs and benefits of *Daphnia* antipredator defense to *Chaoborus* will vary depending on clonal strength of the various defenses as well as the habitat. Nevertheless, this is the first time that the costs and benefits associated with these defenses were measured in nature according to our knowledge. We provide a reference point for costs and benefits involved in inducible defenses of *Daphnia pulex*. The nature of costs owing to upward migration (increased metabolism, competition, and UV radiation) will have to be explored in future.

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Spatial distribution of brown shrimp (*Farfantepenaeus aztecus*) on the northwestern Gulf of Mexico shelf: effects of abundance and hypoxia

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Abstract: We used fishery-independent hydrographic and bottom trawl surveys on the northwestern Gulf of Mexico shelf from 1983–2000 to test for density dependence and effects of hypoxia (dissolved oxygen ≤ 2.0 mg·L^{-1}) on the spatial distribution of brown shrimp (*Farfantepenaeus aztecus*). Spatial distribution of shrimp was positively related to abundance on the Texas shelf but negatively related to abundance on the Louisiana shelf. Density dependence was weak, however, and may have been due to factors other than density-dependent habitat selection. Males were distributed over a broader area and further offshore than were females, though differences in spatial distribution between sexes were not large (~10%–15%). Large-scale hypoxia (up to ~20 000 km^2) on the Louisiana shelf occurs in regions of typically high shrimp density and results in substantial habitat loss (up to ~25% of the Louisiana shelf), with shifts in distribution and associated high densities both inshore and offshore of the hypoxic region. We discuss these results in terms of the generality of density-dependent spatial distributions in marine populations and potential consequences of habitat loss and associated shifts in distribution due to low dissolved oxygen.

Résumé : Des inventaires hydrographiques et des inventaires au chalut indépendants de la pêche commerciale faits dans le nord-ouest du golfe du Mexique de 1983 à 2000 nous ont servi à évaluer la dépendance de la densité, ainsi que les effets de l'hypoxie (oxygène dissous ≤ 2,0 mg·L^{-1}) sur la répartition spatiale de la crevette brune (*Farfantepenaeus aztecus*). Il existe une relation positive entre la répartition spatiale de la crevette et son abondance sur la plate-forme continentale du Texas et une relation négative avec son abondance sur la plate-forme continentale de la Louisiane. Cependant, la dépendance de la densité est faible et peut être due à des facteurs non reliés à un choix d'habitat dépendant de la densité. Les mâles sont répartis sur une plus grande surface et plus au large que les femelles, bien que les différences de répartition spatiale entre les sexes ne soit pas importante (~10–15 %). L'hypoxie à grande échelle (jusqu'à ~20 000 km^2) sur la plate-forme de la Louisiane se produit typiquement dans les zones de forte densité de crevettes et entraîne une perte considérable d'habitat (jusqu'à ~25 % de la plate-forme de la Louisiane); il s'ensuit des modifications de la répartition et des fortes densités qui lui sont associées, tant au large de la région hypoxique que vers la côte. La discussion de ces résultats se fait dans le contexte général des répartitions spatiales dépendantes de la densité chez les populations marines et en rapport avec les conséquences potentielles de la perte d'habitat et des modifications des aires de répartition qui en résultent à cause des faibles teneurs d'oxygène dissous.

[Traduit par la Rédaction]

Introduction

Quantifying spatial patterns of marine fish populations and understanding mechanisms underlying spatial dynamics are important considerations in the management of exploited resources (MacCall 1990; Mason and Brandt 1999; Kruse et al. 2001). For example, changes in spatial distribution may precede major stock declines, potentially serving as early warning signs of future declines in abundance (Gomes et al. 1995; Rose et al. 2000; Overholtz 2002). Alternatively, variation in local abundance may result from shifts in spatial distribution rather than from factors that affect population productivity (Rodríguez-Sánchez et al. 2002). Changes in spatial distribution can alter catchability to commercial fish-

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eries, potentially biasing stock assessments that rely on time series of catch per unit effort (CPUE), whose relationship to population size varies with stock distribution (Paloheimo and Dickie 1964; Winters and Wheeler 1985). For example, contraction of spatial distribution with declining abundance can lead to the maintenance or elevation of commercial CPUE (i.e., hyperaggregation, Hilborn and Walters 1992), overestimation of stock biomass, and underestimation of fishing mortality (Rose and Kulka 1999; Harley et al. 2001). In this paper, we describe spatial patterns of brown shrimp (*Farfantepenaeus aztecus*) on the northwestern Gulf of Mexico shelf and test potential mechanisms underlying annual variation in spatial distribution.

Several studies have documented the expansion of spatial distribution with increases in abundance for marine populations (Marshall and Frank 1994; Petitgas 1998; Anderson and Gregory 2000). Expanding spatial distributions are most often attributed to density-dependent habitat selection with organisms spreading into more marginal habitats as abundance increases, per capita availability of resources in preferred habitats declines, and competition becomes more intense (MacCall 1990; Swain and Wade 1993). Several pelagic species show evidence of density-dependent spatial distributions, and exceptions have yet to be reported (Schneider et al. 1997; Petitgas 1998; Barange et al. 1999). For demersal species, however, evidence for density-dependent spatial distributions has been mixed. Positive density dependence has been reported primarily for gadoids (Atlantic cod, *Gadus morhua*; haddock, *Melanogrammus aeglefinus*) from north temperate marine environments (Swain and Wade 1993; Marshall and Frank 1994; Atkinson et al. 1997). No density dependence has also been reported for other populations of these species (ages 0–2 cod, Schneider et al. 1997; age-4 cod, Anderson and Gregory 2000), as well as other species in similar environments (Murawski and Finn 1988; Swain and Morin 1996; Petitgas 1998). Hannah (1995) reported a positive correlation between spatial distribution and abundance for ocean shrimp (*Pandalus jordani*), but advective–dispersal processes during the pelagic larval phase were considered the primary mechanisms underlying the observed correlation. Contraction of spatial distribution with increasing abundance (negative density dependence) has not been reported. The focus of existing studies on pelagic and north temperate demersal species, as well as potential biases of indices used to quantify spatial distribution (reviewed in Swain and Sinclair 1994; Marshall and Frank 1995; Shepherd and Litvak 2004), raise questions regarding the generality of density-dependent spatial distributions in marine populations. Swain and Morin (1996) suggested further research was necessary to determine the generality of range expansion–contraction with variation in population size.

The distribution of marine fish populations is also related to abiotic factors such as temperature, salinity, and dissolved oxygen (Swartzman et al. 1992; Rose et al. 2000; Begg and Marteinsdottir 2002). Widespread bottom water hypoxia (dissolved oxygen $\leq$ 2.0 mg·L^{-1}) occurs during the summer months (May–August) on the Louisiana shelf as a result of strong salinity stratification and high phytoplankton production arising from freshwater and nutrient inputs from the Mississippi–Atchafalaya river system (Rabalais et al. 2002). In contrast, hypoxia rarely occurs on the Texas shelf because of lower productivity and the diminishing influence of the Mississippi River. Since monitoring began in the early to mid-1980s, the spatial extent of hypoxia has varied from near 0 to >22 000 km^2, with several years of extensive hypoxia in the mid- to late 1990s (Rabalais et al. 2002). Laboratory experiments indicate brown shrimp avoid oxygen levels <2.0 mg·L^{-1} (Renaud 1986; Wannamaker and Rice 2000) and catch rates decline at similar levels (Pavela et al. 1983; Leming and Stuntz 1984; Renaud 1986). Craig et al. (2001) showed that the spatial distribution of demersal biomass on the Louisiana shelf shifted from hypoxic areas ($\leq$2.0 mg·L^{-1}) to areas of intermediate dissolved oxygen (2–5 mg·L^{-1}) when hypoxia was extensive (i.e., 11 000 – 12 000 km^2). While several studies have documented avoidance of low oxygen in the field (Howell and Simpson 1994; Petersen and Pihl 1995; Eby and Crowder 2002), the effects of this avoidance behavior on spatial distribution beyond low oxygen regions has not been investigated. Understanding these effects is important, however, because the impacts of hypoxia on mobile species are likely indirect and mediated by habitat loss and associated shifts in spatial distribution (Breitburg et al. 1999; Craig et al. 2001; Breitburg 2002).

We used long-term, fishery-independent research trawl surveys from 1983 to 2000 to characterize the spatial distribution of brown shrimp during summer (June–July) on the northwestern Gulf of Mexico shelf and to test the effects of variation in abundance (biotic factor) and area of hypoxia (abiotic factor) on shrimp distribution. Spatial distribution also varies between sexes in some species (Jacobson and Hunter 1993; Swain and Morin 1996). We also tested the hypothesis that the distribution of brown shrimp differs between sexes.

Methods

Shrimp life history and data sources

Brown shrimp are an annual species, though some individuals survive longer than a year (e.g., 17 months, Nance et al. 1994; 430 days based on mark–recapture studies, Sheridan et al. 1989). Spawning activity peaks on the shelf from September to November, with a smaller, secondary peak from April to June (Renfro and Brusher 1965; Rogers et al. 1993). Immigration of postlarvae to inshore estuarine nurseries peaks in February–March, with highest densities in nursery habitats during March–April (Baxter 1963; Rogers et al. 1993). Juveniles are demersal and undergo a period of rapid growth (1–3 mm·day^{-1}; Ringo 1965; Parrack 1979) and a gradual emigration to deeper areas of bays and sounds with increasing size (Gaidry and White 1973; Baxter et al. 1988). Subadults generally return to the shelf from May to early June at ages of approximately 3–7 months and sizes of 75–95 mm (Copeland 1965; Matthews 1982). Brown shrimp are broadly distributed on the shelf to depths of 110 m, though highest midsummer densities (June–July) typically occur from 20- to 40-m depth (Matthews 1982; Darnell et al. 1983; Sheridan et al. 1989). Brown shrimp are sexually dimorphic with males reaching a smaller asymptotic size (~170 mm) and possibly maturing earlier than females (~195 mm) (Chavez 1973; Parrack 1979).

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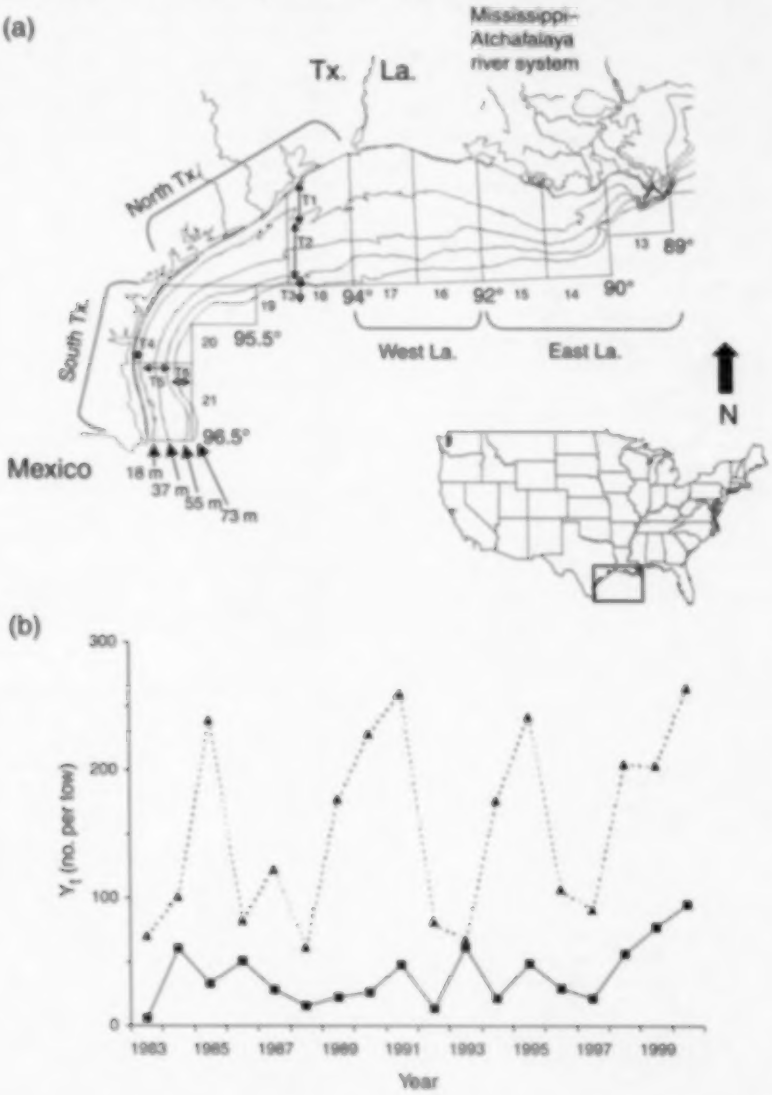
Fig. 1. (*a*) The northwestern Gulf of Mexico (box in inset denotes study location). Degrees refer to the nearest line of longitude (°W), and rectangular bins are labeled with their corresponding statistical zone (13–21). Regions referred to as south Tx., north Tx., east La., and west La. are noted (Tx., Texas; La., Louisiana). Arrows show the relative location of six regions of the Texas shelf: T1 = zones 18–19, 3–18 m (7537 km^2); T2 = zones 18–19, 18–64 m (18 270 km^2); T3 = zones 18–19, 64–110 m (1410 km^2); T4 = zones 20–21, 3–18 m (1916 km^2); T5 = zones 20–21, 18–64 m (13 493 km^2); T6 = zones 20–21, 64–110 m (4565 km^2). (*b*) Relative abundance (stratified mean catch per standard tow) of brown shrimp (*Farfantepenaeus aztecus*) (pooled over sexes) for Texas (statistical zones 18–21, dotted line) and Louisiana (statistical zones 13–17, solid line) over the survey time series.



An annual bottom trawl survey has been conducted during June–July in the northwestern Gulf of Mexico since 1983 under the Southeast Area Monitoring and Assessment Program (SEAMAP) (Fig. 1; Eldridge 1988). From 1987 to 2000, surveys used a stratified random design based on depth, geographic location, and time of day (day–night). Each survey was conducted by the R/V *Oregon II* using a 12.8-m shrimp trawl with mud rollers and 2.4 m × 1 m wooden chained doors. Sampling was also conducted by two additional vessels, the R/V *Pelican* and the R/V *Tommy Munro*, using the same gear and sampling protocol. Comparative experiments among these three vessels revealed no differences in catch rates (Pellegrin 2004). No sampling was conducted inshore of 4 m because of depth limitations of the survey vessels. Equal numbers of day and night tows were conducted perpendicular to the depth contours defining each stratum at a speed of 3 knots. Catch rates of shrimp tend to be higher at night than during the day (Craig and Crowder 2005). However, because there is equal day and night sampling effort within each stratum, we as-

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sumed diel differences in catchability were constant over the 1987–2000 time period, so that survey indices of relative abundance and spatial distribution reflected annual variation in actual abundance and distribution. Bottom measurements of temperature, salinity, and dissolved oxygen were taken at each station prior to the trawl. All shrimp were sexed, counted, and 200 per station were measured (tip of rostrum to end of telson). Catches were adjusted to a standard tow length of 2.8 km (~1.5 nautical miles) prior to analysis. The number of stations ranged from 79 to 215 (average = 193) per survey.

From 1983 to 1986, all trawling was conducted at night so that indices of abundance and spatial distribution estimated for these years were not directly comparable to the 1987–2000 time period. To address this, we adjusted annual indices for each year from 1983 to 1986 to make them comparable with the longer portion of the time series (1987–2000). First, we calculated indices for only the night samples and then only the day samples for each year from 1987 to 2000 when sampling effort during day and night was approximately equal. Then we calculated indices based on the night-only sampling for each year from 1983 to 1986. We used the ratio of day to night indices from the 1987–2000 period to correct those for each year from 1983 to 1986. To account for variation among years in these ratios, we used a Monte Carlo approach, where the distribution of ratios of day to night indices was sampled 1000 times and a corresponding new estimate was calculated for each year from 1983 to 1986. The average of these 1000 corrected values was then used in the analyses below. Adjustments for these changes are further described in Craig (2001) and had little effect on results presented here. Additional details regarding vessel characteristics, survey design, and sampling procedures can be found in Eldridge (1988), Nichols et al. (1987, 1990), and the annual SEAMAP atlases (e.g., Rester et al. 2004).

Analyses

Since 1981, Texas waters (statistical zones 18–21, Fig. 1*a*) have been closed to shrimping prior to and during the SEAMAP survey (Klima et al. 1982). In contrast, shrimping is allowed in Louisiana waters (statistical zones 13–17) and occurs outside the survey region as shrimp emigrate from inshore estuaries and in nearshore waters of the shelf (generally <20-m depth). The presence or absence of shrimp harvest results in striking differences in survey catch rates between the two regions, with relative abundance off Texas on average nearly fivefold that off Louisiana (Fig. 1*b*). Given the potential bias from pooling data over these regions, we tested the response of shrimp distribution to variation in abundance separately for the portions of the survey conducted off Louisiana and off Texas. We expected density dependence in spatial distribution, if it exists, to be stronger off Texas than off Louisiana given the higher densities of shrimp there.

Abundance

We used the stratified mean catch per standard tow (Y_t) as an index of shrimp abundance:

$$(1) \qquad Y_t = \sum_{h=1}^{L}\sum_{i=1}^{K} T_h W_i y_{hit}$$

where W_i is the proportion of the survey area in stratum i, K is the number of strata, T_h is the proportion of the survey in time period h (day = 14 h or night = 8 h), L is the number of time periods, and y_{hit} is the mean catch per standard tow of shrimp during time period h in stratum i for year t. We calculated this index separately for Texas and Louisiana waters for each sex and year. Mean catch rates estimated using the Delta method, a model-based index of abundance (Smith 1990; Pennington 1996), were highly correlated with Y_t (females: $r^2 = 0.74$; males: $r^2 = 0.89$; both $n = 17$, $P < 0.001$) and gave similar results (Craig 2001). In addition, annual CPUE in the Gulf-wide commercial shrimp fishery (Nance 2001) was positively correlated with both estimates of Y_t (pooled over sexes) (Louisiana, $r^2 = 0.38$, $P = 0.008$, $n = 17$; Texas, $r^2 = 0.58$, $P < 0.001$, $n = 17$). These correlations suggest survey indices of relative abundance are good indicators of annual patterns in shrimp abundance.

Tests for density-dependent spatial distribution

We used two approaches to test for density-dependent spatial distributions of brown shrimp (Swain and Sinclair 1994; Marshall and Frank 1995). First, we tested for a positive correlation between annual indices of distributional area (or the area over which a specified percentage of shrimp are distributed) and relative abundance (Swain and Sinclair 1994). Second, we tested for regional variation in the rate of local density change, predicting that density should change less in regions that are always inhabited (i.e., preferred) than in regions that are only inhabited when abundance is high and distribution expands there (i.e., marginal) (Marshall and Frank 1995). Our approach is similar to that of Swain and Morin (1996), and additional methodological details can be found there.

Distributional area on the Texas shelf

We estimated the distributional area of female and male shrimp as the minimum area over which a specified percentage of shrimp were distributed (Swain and Sinclair 1994). First, we calculated catch-weighted cumulative distribution functions ($F(c)$) of shrimp catch as follows:

$$(2) \qquad F(c) = 100\,\frac{\sum_{h=1}^{L}\sum_{i=1}^{K}\sum_{j=1}^{n_i}\frac{T_h A_i}{n_i} X_{hij}\, I}{\sum_{h=1}^{L}\sum_{i=1}^{K}\sum_{j=1}^{n_i}\frac{A_i}{n_i} X_{hij}}$$

where $I = 1$ if $X_{hij} \le c$ and $I = 0$ otherwise. T_h, L, and K are as defined above, n_i is the number of tows in stratum i, A_i is the area of stratum i, X_{hij} is the number of shrimp caught in tow j in stratum i during time period h, and I is a binary variable (1 or 0) corresponding to the specified level of shrimp density c. We then calculated cumulative area ($G(c)$) in relation to shrimp catch as follows:

$$(3) \qquad G(c) = \sum_{h=1}^{L}\sum_{i=1}^{K}\sum_{j=1}^{n_i}\frac{A_i}{n_i} I$$

where $I = 1$ if $X_{hij} \le c$ and $I = 0$ otherwise.

We estimated the minimum area over which the most densely distributed 95% (Area 95), 75% (Area 75), and 50% (Area 50) of shrimp occurred and standardized these indices

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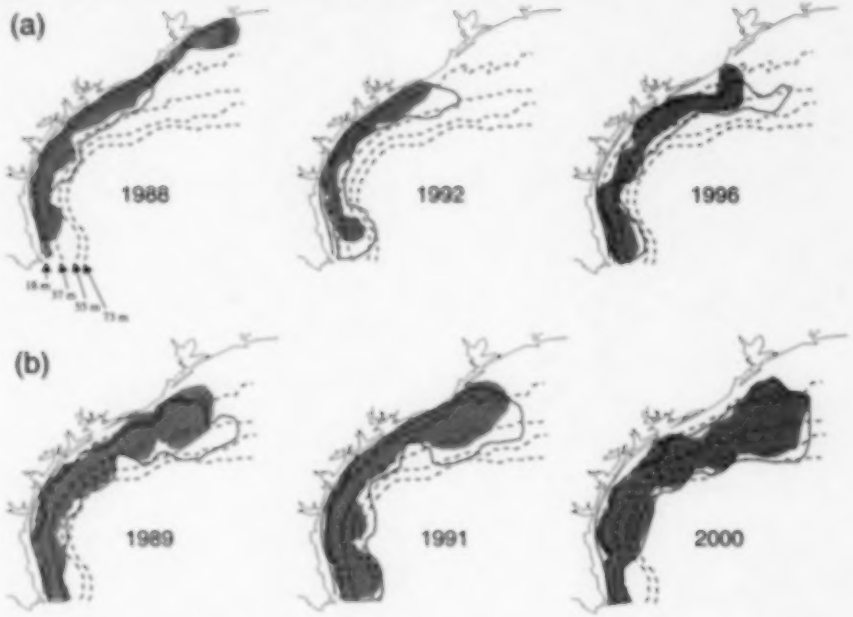
Fig. 2. Examples of annual variation in the spatial distribution of brown shrimp (*Farfantepenaeus aztecus*) on the Texas shelf during years of (*a*) low and (*b*) high abundance. Interpolations refer to the area over which the 95th percentile of female (solid gray) and male (black outline) shrimp catches was distributed. Dashed lines represent depth contours.



to the total survey area off Texas (47 196 km^2). We tested the effect of relative abundance on distributional area for each sex and percentile of shrimp distribution using Pearson product moment correlations. We then used a general linear model with terms for relative abundance and sex to test for differences between sexes in spatial distribution and interaction effects.

We mapped the distribution of female and male shrimp on the Texas shelf for representative high and low abundance years. All standardized catches were projected in Albers equal area coordinate system prior to mapping by universal kriging with a quadratic drift component using the Kriging Interpolator 3.2 SA extension in ArcView (ESRI, Redlands, California). Interpolations used the 15 nearest samples within a search radius of 100 km.

Regional variation in distribution and rates of local density change on the Texas shelf

As a second test of density-dependent spatial distributions, we described regional differences in the relationship between local density and relative abundance of shrimp on the Texas shelf (Marshall and Frank 1995). We pooled strata into six regions (T1–T6, Fig. 1*a*) and calculated the mean catch rate in each region for each sex and year. We assumed the relationship between local density and abundance was described by a power function (Myers and Stokes 1989):

$$(4) \qquad y_{jt} = \alpha_j Y_t^{\beta_j}$$

where y_{jt} is the mean female or male shrimp catch in region j for year t, Y_t is the stratified mean catch rate of female or male shrimp on the Texas shelf in year t, and β_j describes how regional catch rates vary with relative abundance. We estimated β for each region separately for each sex using the following generalized linear model:

$$(5) \qquad E(y_{jt}) = \mu_{jt} = \exp(a_j + \beta_j \ln Y_t)$$

where a_j is the log of α_j above. We then tested for regional variation in β using a generalized linear model with terms for region, relative abundance, and their interaction.

Interpretation of regional variation in the rate of local density change is difficult without knowledge of the distribution of resources for which shrimp presumably compete. Swain and Morin (1996) assumed that variation in local abundance among regions maps the distribution of preferred habitats when abundance, and presumably the intensity of competition, is low. Similarly, we calculated the mean catch rate of female and male shrimp separately for each region of the Texas shelf (Fig. 1*a*) over the 6 years of lowest abundance as an index of preferred habitat. We then tested for a relationship between this index and β, predicting that preferred regions would have low annual variation in local abundance compared with marginal regions.

To determine if regional differences in catch rates varied between high and low abundance periods, we also calculated mean catch rates in each region over the 6 years of highest relative abundance. We then tested for a significant interaction effect in a generalized linear model, with terms for abundance period (high, low) and region (T1–T6) as fixed effects and year nested within abundance period as a random effect. For the three analyses described above (estimating β, regional variation in β, and regional variation in catch rates between high and low abundance periods), we used quasi-likelihood estimation assuming an extra-Poisson error model in S-plus 2000 (Venables and Ripley 1999).

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Fig. 3. Pearson's correlations between indices of brown shrimp (*Farfantepenaeus aztecus*) distribution for (*a*) Area 95, (*b*) Area 75, and (*c*) Area 50 and relative abundance (Y_t) on the Texas shelf. Solid lines indicate significant ($P < 0.05$) or marginally significant ($P < 0.1$) relationships, and dashed lines indicate nonsignificant relationships. Females, ■; males, □. Note differences in scale of *y* axes.

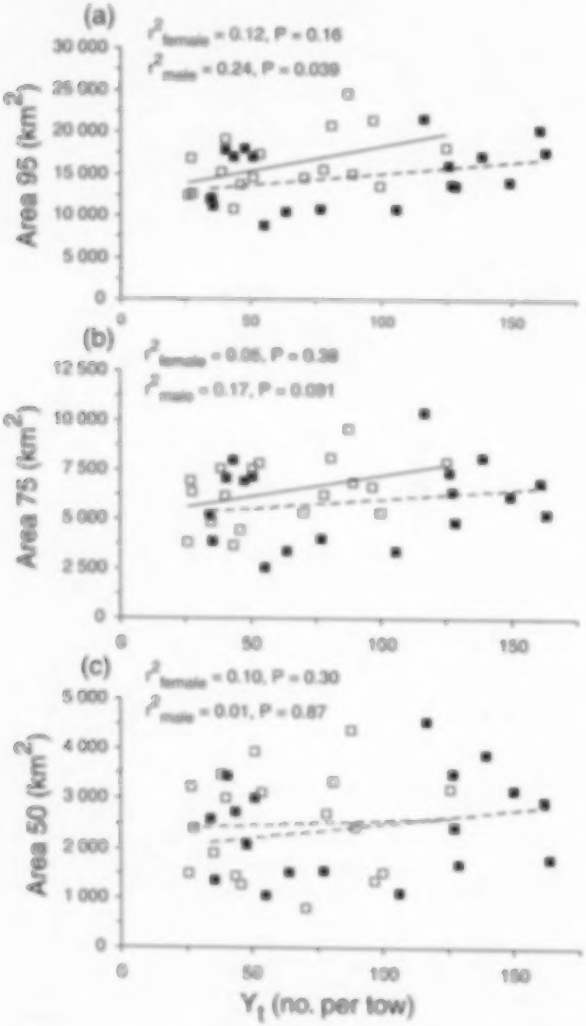
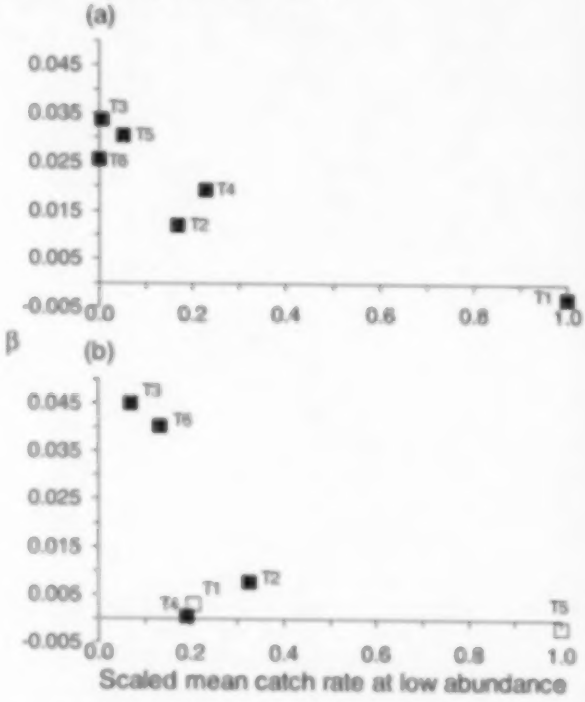

(a)
r^2_{female} = 0.12, P = 0.16
r^2_{male} = 0.24, P = 0.039
Area 95 (km^2)
(b)
r^2_{female} = 0.05, P = 0.38
r^2_{male} = 0.17, P = 0.091
Area 75 (km^2)
(c)
r^2_{female} = 0.10, P = 0.30
r^2_{male} = 0.01, P = 0.87
Area 50 (km^2)
Y_t (no. per tow)

Fig. 4. Estimates of rate of local density change (β) for (*a*) female and (*b*) male brown shrimp (*Farfantepenaeus aztecus*) in six regions of the Texas shelf (T1–T6) in relation to the mean scaled catch rate over the 6 years of lowest abundance in each region. Solid squares are significant values ($P > 0.05$) and open squares are nonsignificant ($P > 0.05$).



Distributional area on the Louisiana shelf

We related variation in the spatial distribution of shrimp on the Louisiana shelf to variation in both the area of hypoxia and relative abundance. We interpolated bottom dissolved oxygen on the Louisiana shelf using the same mapping procedure described previously and calculated the area with dissolved oxygen levels ≤2.0 mg·L^{-1}. We then estimated the area of the Louisiana shelf occupied by the most densely distributed 95%, 90%, and 75% of shrimp as described previously. We tested for significant partial correlations using a general linear model, with terms for the area of hypoxia and relative abundance fitted separately for each sex and measure of shrimp distribution. To assess differences in distribution between sexes as well as interaction effects, we used a general linear model with terms for sex, area of hypoxia, relative abundance, and their interactions (all two-way and three-way). We did not test for regional variation in rates of local density change of shrimp on the Louisiana shelf (as for the Texas shelf) because of the strong and confounding effect of hypoxia on local catch rates (see Results).

Shifts in distribution in relation to hypoxia

To characterize shifts in the spatial distribution of shrimp in response to hypoxia, we mapped the distribution of females and males separately for both severe (1993, 1995, 1996, and 1997; 14 988 – 17 084 km^2, ≤2.0 mg·L^{-1}) and moderate (1983, 1987, 1988, 2000; 2155–4350 km^2, ≤2.0 mg·L^{-1}) hypoxia periods. To standardize data over years, we divided each catch (ln-transformed) by the stratified mean catch rate in that year and multiplied by the average stratified mean catch rate over all 8 years. We also interpolated shrimp catch for each sex for two individual years, 1987 and 1997, when the area of hypoxia differed by nearly fourfold (4350 km^2 vs. 16 150 km^2). Mapping and interpolation procedures were identical to those described previously.

We tested for differences in the distribution of shrimp on the Louisiana shelf between severe and moderate hypoxia periods using a generalized linear model. We restratified the data into six depth bins (0–9, 9–18, 18–27, 27–37, 37–64,

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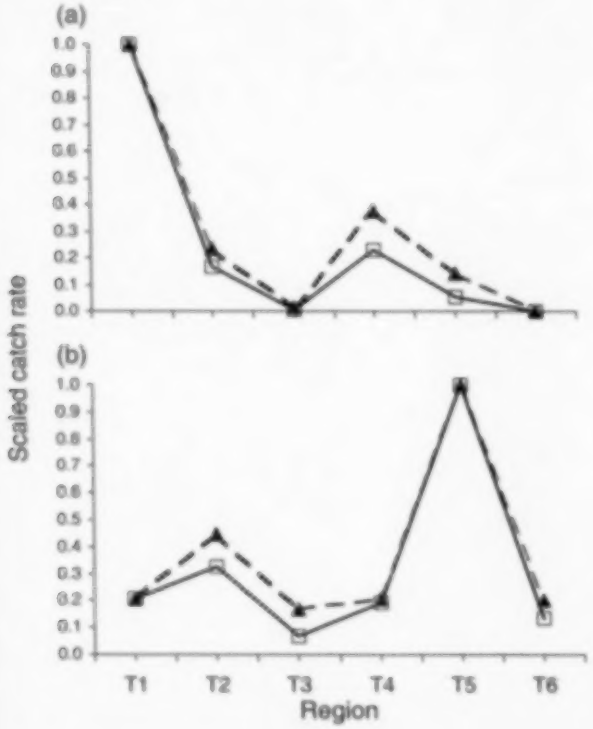
Table 1. Tests for regional variation in (*i*) the rate of local density change (β) and (*ii*) distribution between high and low abundance periods for female and male brown shrimp (*Farfantepenaeus aztecus*) on the Texas shelf.

	Female		Male	
Model	R^2_{model}	$\%R^2_{interaction}$	R^2_{model}	$\%R^2_{interaction}$
Regional β (n = 1621)	0.424 (<0.001)	3.3 (0.041)	0.412 (<0.001)	5.3 (0.026)
Abundance period (n = 1016)	0.462 (<0.001)	2.3 (0.059)	0.464 (0.001)	3.2 (0.006)

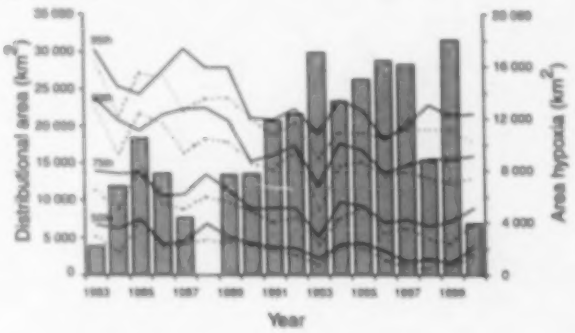
Note: R^2_{model} is the fraction of the deviance explained by the full model, and $\%R^2_{interaction}$ is the percentage of this value attributable to the interaction term. Sample sizes are 1621 and 1016 for the two models, respectively. P values are given in parentheses.

Fig. 5. Mean catch rates of (*a*) female and (*b*) male brown shrimp (*Farfantepenaeus aztecus*) by region of the Texas shelf for low (□, solid line) and high (▲, dotted line) abundance periods. Mean catch rates are scaled by the maximum mean in each abundance period.



and 64–110 m) for the eastern (statistical zones 13–15) and western (statistical zones 16–17) regions of the Louisiana shelf (Fig. 1*a*) and calculated the mean catch rate of shrimp for each stratum separately for each sex. The model included terms for region, depth bin nested within region, hypoxia period, year nested within hypoxia period (random effect), region × hypoxia period interaction, and depth bin nested within region × hypoxia period interaction. To assess the significance of differences in the spatial distribution of shrimp between severe and moderate hypoxia periods, we tested for interaction effects (region × hypoxia period and depth bin nested within region × hypoxia period) in the above model.

Fig. 6. Annual variation in indices of distributional area of female (broken line) and male (solid line) brown shrimp (*Farfantepenaeus aztecus*) and area of hypoxia (gray bars, dissolved oxygen ≤ 2.0 mg·L^{-1}) on the Louisiana shelf during July. 95th, 90th, 75th, and 50th refer to percentiles of shrimp spatial distribution.



Results

Distributional area on the Texas shelf

Brown shrimp were distributed along nearly the entire Texas coast from shore to depths of up to 110 m (Fig. 2). During high abundance years, the distribution of both sexes extended further offshore. Correlations between distributional area and abundance were in the predicted positive direction for both sexes and all percentiles of shrimp distribution, but were relatively weak and only significant or marginally significant for Area 95 and Area 75 of males (Fig. 3). Males were distributed over a larger area (~10%) than females (Area 95, $F_{[1,32]} = 7.07$, $P = 0.012$; Area 75, $F_{[1,32]} = 7.85$, $P = 0.009$; Fig. 2), and correlations with abundance were stronger despite generally lower male abundance (Fig. 3). Interaction effects between sex and relative abundance on distributional area were not significant (all $P > 0.56$).

Regional variation in rates of local density change and distribution on the Texas shelf

Regional variation in the rate of change in local shrimp density (i.e., β) was consistent with results based on distributional area, suggesting relatively weak density dependence (Fig. 4). β was lowest in regions where shrimp density tended to be relatively high, indicating slower rates of density change in these presumably preferred habitats. For females, slopes were significant for all but one region (T6) and were generally highest for midshelf and offshore regions

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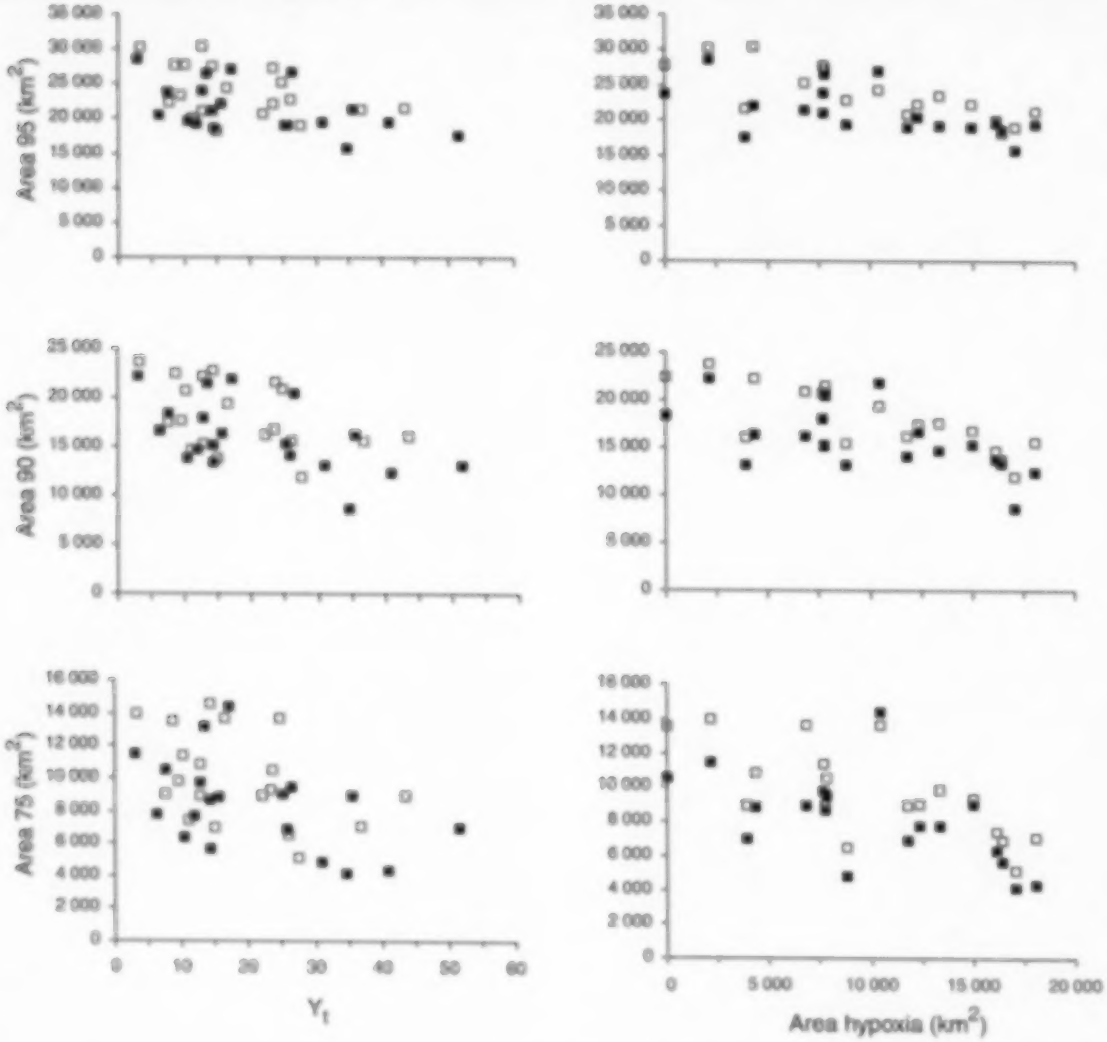
Fig. 7. Relationship between indices of distributional area (Area 95, Area 90, and Area 75) and relative abundance (Y_t) or area of hypoxia for female (■) and male (□) brown shrimp (*Farfantepenaeus aztecus*) on the Louisiana shelf. Note the difference in *y* axis scale for different percentiles of shrimp distribution.



(T3, T5; Fig. 4*a*). For males, slopes were significant for three regions and tended to be highest offshore (T3, T6; Fig. 4*b*). There was a negative relationship between β and the mean regional catch rate of shrimp during the 6 years of lowest abundance that was significant for females (r = –0.88, P = 0.021) but not for males (r = –0.57, P = 0.24). As for analyses of distributional area, regional variation in the rate of local density change accounted for a small, though significant, proportion of the explained variation in shrimp catch rates (~3%–5%, Table 1).

There were differences in regional patterns of distribution between female and male shrimp (Fig. 5). Catch rates of females were highest in nearshore regions (T1 and T4), particularly on the north Texas shelf (T1), whereas catch rates of males were highest in midshelf regions (T2 and T5), particularly on the south Texas shelf (T5). During years of high abundance, catch rates of females increased on the south Texas shelf, particularly in nearshore and midshelf regions (T4, T5), whereas catch rates of males increased on the north Texas shelf, particularly in midshelf and offshore regions (T2, T3). Regional variation in catch rates between high and low abundance periods was significant for males and marginally significant for females, but the amount of variation explained by this interaction was small (~2%–3%, Table 1).

Distributional area on the Louisiana shelf

The area of the Louisiana shelf occupied by brown shrimp declined by about 25% from the mid- to late 1980s to the mid- to late 1990s (e.g., Area 95: females, r = –0.78, P = 0.001; males, r = –0.71, P = 0.008), while the area of hypoxia increased over the same time period (r = 0.55, P =

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Table 2. Partial R^2 (as a fraction of the model R^2) between distributional area and either abundance or area of hypoxia on the Louisiana shelf for three percentiles of female and male brown shrimp (*Farfantepenaeus aztecus*) distribution.

	Multivariate models partial R^2		
	Model R^2	Abundance	Hypoxia
Female			
Area 95	0.482	0.154 (0.052)	0.252 (0.017)
Area 90	0.529	0.189 (0.027)	0.256 (0.012)
Area 75	0.467	0.144 (0.062)	0.250 (0.018)
Male			
Area 95	0.640	0.060 (0.135)	0.480 (0.001)
Area 90	0.653	0.073 (0.096)	0.472 (0.001)
Area 75	0.573	0.073 (0.130)	0.401 (0.002)

Note: All correlations are negative. *P* values are given in parentheses.

Table 3. Effects of sex, area of hypoxia, and abundance on distributional area (Area 95, Area 90, or Area 75) of brown shrimp (*Farfantepenaeus aztecus*) on the Louisiana shelf.

	Area 95	Area 90	Area 75
Model R^2	0.66***	0.65***	0.57***
% Model R^2			
Sex	12.70**	10.60**	12.70**
Hypoxia	48.50***	49.60***	51.10***
Abundance	14.0***	18.30***	17.10**
Sex × Abundance	0.10	0.27	0.03
Sex × Hypoxia	1.28	0.89	0.84
Abundance × Hypoxia	6.99*	1.53	0.11
Sex × Abundance × Hypoxia	0.57	1.41	0.70

Note: The percentage of the model R^2 accounted for by each term is shown (Venables and Ripley 1999). ***, $P < 0.01$; **, $P < 0.05$; *, $P < 0.1$. No asterisk indicates that the term was not significant ($P > 0$). Sample size = 36.

0.018) (Fig. 6). Distributional area of both sexes was negatively correlated with both relative abundance (Y_r) and area of hypoxia (Fig. 7). For females, the partial effect of abundance explained 14%–19% of the variation in spatial distribution and was significant or marginally so, while the partial effect of hypoxia explained 25%–26% of the variation and was always significant(Table 2). For males, the partial effect of abundance explained only 6%–7% of the variation and was never significant, while the partial effect of hypoxia explained 40%–48% of the variation and was highly significant in all cases (Table 2).

Models including the effects of sex, area of hypoxia, relative abundance, and their interactions explained 57%–66% of the variation in distributional area on the Louisiana shelf, depending on the percentile of shrimp distribution (Table 3). All three main effects were significant. About 10%–13% of the explained variation in distribution was attributable to sex, with males distributed over a greater area than were females in 16 of 18 years (Fig. 6). Interaction terms were generally not significant and explained a small amount of the model R^2 (<7%; Table 3).

Shifts in distribution in response to hypoxia

The depth distribution of shrimp on the Louisiana shelf differed considerably between severe and moderate hypoxia periods (Fig. 8). With moderate hypoxia, scaled catch rates were highest from shore to 27 m, declining with further increases in depth. In contrast, with severe hypoxia, scaled catch rates remained very high inshore, declined considerably at intermediate depths (i.e., 9–27 m), and increased immediately offshore (i.e., 27–43 m). This effect of hypoxia on depth distribution was highly significant for both sexes (Table 4), indicating shrimp are displaced by low oxygen over large areas of the shelf and occur at relatively high densities inshore and offshore of the hypoxic region. Similar to the Texas shelf, the distribution of males was slightly greater than that for females, extending further offshore during both high and low hypoxia periods (Fig. 8).

The effect of hypoxia on shrimp distribution was also apparent from interpolated maps of shrimp catches (Fig. 9). When hypoxia extended over a relatively small area, shrimp were distributed throughout the shelf, with multiple patches of high density both inshore and offshore of hypoxic regions (Figs. 9*a*, 9*b*). When hypoxia was severe, high densities of both sexes occurred inshore, almost no shrimp occupied waters from about 9- to 18-m depth, and large, high-density aggregations were evident just offshore of the hypoxic region (Figs. 9*c*, 9*d*).

Discussion

While early studies suggested that density-dependent spatial distributions might be a general feature of marine fish populations (e.g., Winters and Wheeler 1985), results from more recent studies have been mixed. Positive density dependence has been reported for several marine populations (Crecco and Overholtz 1990; Petitgas 1998; Anderson and Gregory 2000) but not others (Swain and Morin 1996; Petitgas 1998). Both positive density dependence (Swain and Wade 1993; Atkinson et al. 1997; Anderson and Gregory 2000) and no density dependence (Murawski and Finn 1988; Schneider et al. 1997) have even been reported among different populations and age classes of the same species (i.e., Atlantic cod). Both analytic approaches reported here suggested that spatial distribution of brown shrimp on the Texas shelf expanded in years of high abundance, but relationships between distribution and abundance were weak and not always substantial. For comparison, abundance of cod in the Gulf of St. Lawrence varied fourfold from 1971 to 1991 and explained 63%–94% of the variation in cod distribution (Swain and Wade 1993), while indices of shrimp abundance on the Texas shelf varied fivefold from 1983 to 2000 but explained less than 24% of the variation in shrimp distribution. Similarly, a twofold increase in abundance of age-2 cod resulted in a 70% increase in area occupied on the Newfoundland shelf (Anderson and Gregory 2000), while a similar increase in shrimp abundance led to a 10%–20% increase in area occupied on the Texas shelf. We expected density dependence to be particularly evident on the Texas shelf given that harvest restrictions result in relatively high shrimp densities. Even so, our results indicate at best weak, positive density dependence in the spatial distribution of brown shrimp off Texas.

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Fig. 8. Mean catch rates of female (solid line, ■) and male (broken line, □) brown shrimp (*Farfantepenaeus aztecus*) by region and depth bin on the Louisiana shelf during moderate (1983, 1987, 1988, 2000) and severe (1993, 1995, 1996, 1997) hypoxia periods. (*a*) Eastern shelf, moderate hypoxia, (*b*) western shelf, moderate hypoxia, (*c*) eastern shelf, severe hypoxia, (*d*) western shelf, severe hypoxia. Mean catch rates are scaled by the maximum mean in each hypoxia period. Eastern shelf = statistical zones 13–15; western shelf = statistical zones 16–17.

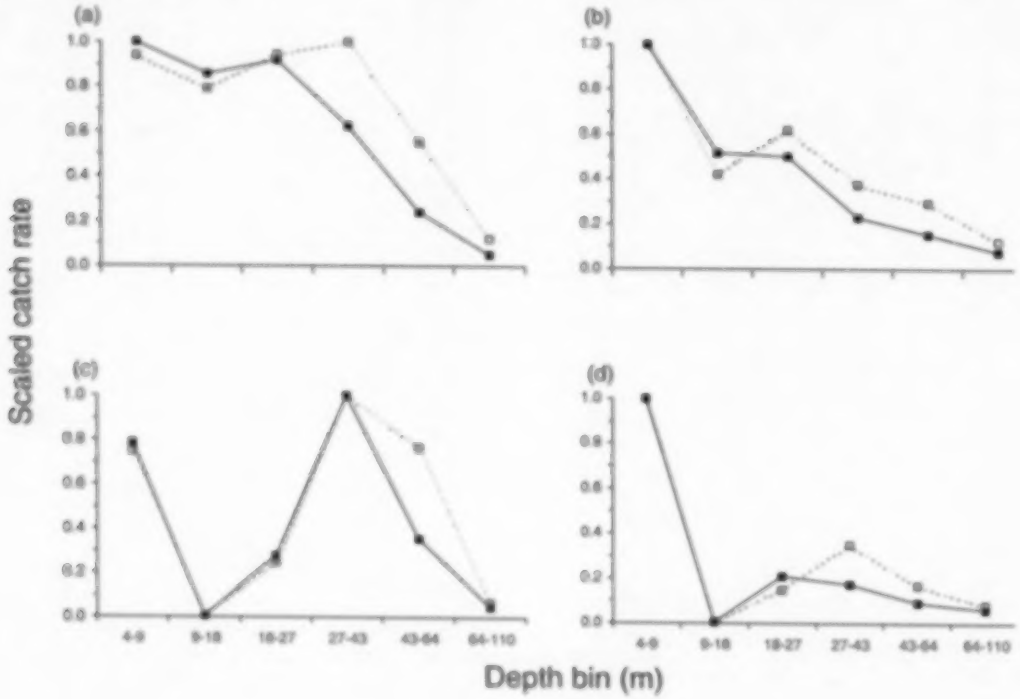

Table 4. Models of the effects of hypoxia on the spatial distribution of brown shrimp (*Farfantepenaeus aztecus*) on the Louisiana shelf.

	Female	Male
Model R^2	0.80 (<0.001)	0.74 (<0.001)
% Model R^2		
Region	4.30 (0.002)	6.70 (0.001)
Hypoxia period	5.70 (0.003)	4.70 (0.006)
Depth(region)	48.10 (<0.001)	45.40 (<0.001)
Year(hypoxia period)	24.50 (<0.001)	22.50 (<0.001)
Region × hypoxia period	0.230 (0.45)	0.140 (0.63)
Depth(region) × hypoxia period	17.10 (0.001)	20.60 (<0.001)

Note: The percentage of the model R^2 accounted for by each term is shown. *P* values are given in parentheses. Sample size = 96.

Shrimp distribution expanded offshore when abundance was high, suggesting variation in the timing and magnitude of emigration from inshore estuarine nursery areas as an alternative mechanism (to density-dependent habitat selection) underlying the positive relationship between distribution and abundance off Texas. Emigration from inshore estuaries peaks during May and declines rapidly by early June (Copeland 1965; Matthews 1982), though little is known about the duration of emigration or subsequent movement rates to the shelf. The expanded offshore distribution of shrimp during years of high abundance may reflect an earlier or more extended emigration period from inshore to offshore habitats rather than density-dependent habitat selection occurring on the shelf.

In contrast with results for the Texas shelf, spatial distribution of shrimp off Louisiana was negatively related to abundance. The possibility of negative density dependence was acknowledged by Marshall and Frank (1995), though examples and potential underlying mechanisms have not been reported. One possibility is that habitat is not limited for shrimp on the Louisiana shelf and intraspecific competition is weak. If this is the case, and high abundance enhances aggregative tendencies, then shrimp may be distributed over relatively smaller areas when abundance is high. A second possibility is that the spatial distribution of shrimp is related to the geographic location of inshore, estuarine nursery habitats that are the source of recruits. If shrimp remain in the general vicinity of estuarine outlets after recruiting to the shelf, and one or a few estuaries in close geographic proximity supply the majority of recruits, then spatial distribution may be relatively small despite high shrimp abundance. Likewise, if the supply of recruits from inshore nurseries along the coast is uniformly low, then distributional area (defined as the area occupied by some proportion of shrimp) may be large despite low abundance if shrimp remain in the general vicinity of their estuary of origin. Understanding the movement capacities and migratory patterns of shrimp as well as the production dynamics of inshore nurseries is im-

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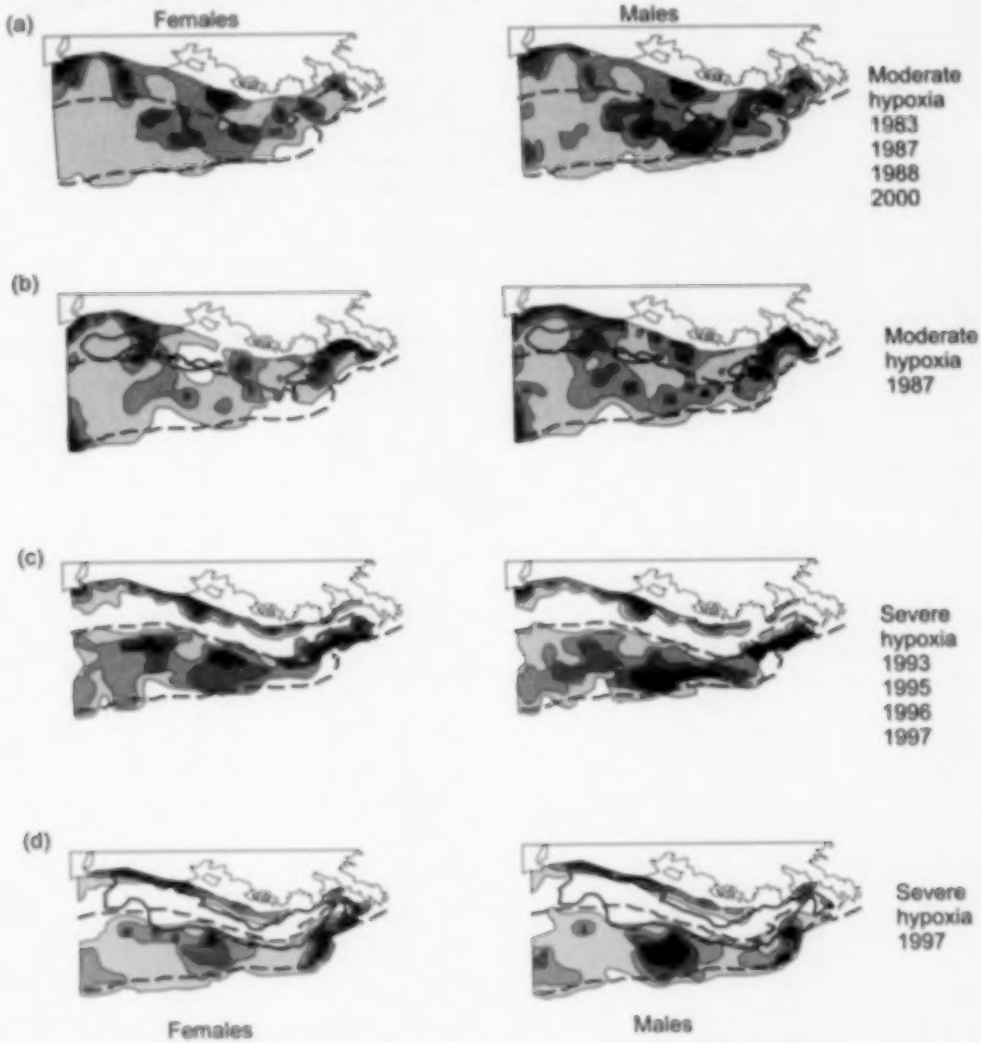
Fig. 9. Distribution of brown shrimp (*Farfantepenaeus aztecus*) on the Louisiana shelf during moderate and severe hypoxia periods and years. (*a*) Moderate hypoxia period (1983, 1987, 1988, 2000); (*b*) moderate hypoxia year (1987); (*c*) severe hypoxia period (1993, 1995, 1996, 1997); (*d*) severe hypoxia year (1997). Dashed lines are the 18- and 73-m depth contours. Solid lines (panels *b*, *d*) enclose areas where bottom dissolved oxygen is ≤2.0 mg·L^{-1}. Solid colors refer to the 25th, 50th, 75th, and 95th percentiles of shrimp distribution (darkest to lightest shading, respectively).



portant for evaluating factors underlying variation in abundance and spatial distribution on the shelf.

The relationship between spatial distribution and abundance off Louisiana is confounded to some extent by habitat loss due to large-scale hypoxia. While relative abundance still accounted for a substantial amount of the variation in spatial distribution (of females) after accounting for the area of hypoxia, models including both effects accounted for only one-half to two-thirds of the variation in shrimp distribution, suggesting other factors not considered are important. Unmeasured factors potentially correlated with abundance or hypoxia may result in a spurious negative correlation between spatial distribution and abundance (Shepherd and Litvak 2004). For example, hypoxia may alter the catchability of shrimp to the survey. This could occur if shrimp are herded into relatively small areas as they avoid low oxygen (Craig and Crowder 2005) or if occupying low-oxygen waters impedes trawl avoidance responses (Baden et al. 1990). The combination of habitat loss (decreased spatial distribution) and increased catchability (increased abundance) associated with hypoxia could account for the observed negative relationship between spatial distribution and abundance off Louisiana. Whatever the case, key assumptions of ideal free distribution theory on which density-dependent habitat selection is based (freedom to choose habitats, knowledge of habitat suitability, no travel costs, etc.)

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are likely violated on the Louisiana shelf where shrimp are displaced inshore and offshore of the hypoxic region over large areas of the shelf.

Male shrimp were distributed farther offshore and over a slightly greater area than were females off Texas and Louisiana. This difference in spatial distribution was not likely because of differences in abundance between the sexes or because of restriction of the smaller sex to a smaller foraging area, since females were both more abundant and larger than males but distributed over a smaller area. One possibility is that females have a stronger preference for warm inshore waters than do males to facilitate rapid growth and future egg production. A second possibility is that females migrate from inshore estuaries later than do males, such that fewer females occur offshore relative to males. Males were most abundant in midregions of the south Texas shelf, whereas females were most abundant in inshore regions of the north Texas shelf. Limited tagging data suggests an offshore and southwestward movement of shrimp during summer (Sheridan et al. 1987, 1989). Earlier emigration of males from inshore estuaries combined with a gradual offshore and southwestward movement on the shelf is consistent with these observed regional differences in abundance.

Hypoxia can extend over large portions of the Louisiana shelf (~15 000 – 20 000 km^2), with suggestions of a worsening trend over the last 25–35 years associated with increased nutrient loading to the Mississippi–Atchafalaya river system (Rabalais et al. 2002; Scavia et al. 2003). Moderate levels of nutrient loading may lead to increased benthic production and associated habitat quality for shrimp, as suggested by the typically high shrimp densities in nearshore regions of the shelf (Moore et al. 1970; Darnell et al. 1983). Shrimp avoid these same regions when oxygen levels are low, however, suggesting that hypoxia not only results in substantial habitat loss but possibly loss of the highest quality habitats on the shelf.

Habitat loss and shifts in spatial distribution over such large areas may lead to a variety of associated effects with the potential to impact shrimp production, though these are largely unknown for the northwestern Gulf of Mexico. Zimmerman and Nance (2001) suggested the migration of shrimp to offshore waters is blocked when hypoxia extends over large portions of the Louisiana coast. Our results provide only partial support for this hypothesis. During years of severe hypoxia, high shrimp densities occurred both inshore and offshore of the hypoxic region, suggesting that while the offshore movement of shrimp emigrating subsequent to the onset of hypoxia may be impeded, shrimp already on the shelf may be displaced further offshore. Given declining temperatures and possibly declining food resources with increasing depth, as well as relatively high inshore temperatures, such habitat loss and shifts in spatial distribution may have consequences for shrimp energy budgets and associated growth (Craig and Crowder 2005). Likewise, hypoxia-induced shifts in spatial distribution have been shown to modify trophic interactions in other systems (Breitburg et al. 1997, 1999). These potential effects of habitat loss due to hypoxia are the subjects of ongoing studies.

In summary, our results suggest weak density-dependent effects and strong effects of hypoxia on the spatial distribution of brown shrimp. Relationships between spatial distribution and relative abundance were in opposite directions for different portions of the geographic range (Texas vs. Louisiana), suggesting the spatial scale of similar analyses should be carefully considered. Additional studies, particularly of demersal species in subtemperate and tropical ecosystems, are necessary to further evaluate the generality and strength of density-dependent spatial distributions in marine populations. The hypoxic region in the northwestern Gulf of Mexico is one of the largest such areas known (Rabalais et al. 2002) and results in considerable habitat loss for species on the shelf. Because mobile species are typically able to avoid low-oxygen waters, the ability to determine whether such large-scale habitat loss has population-level consequences will require linking shifts in spatial distribution to growth, mortality, and reproductive processes.

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Periphyton, water quality, and land use at multiple spatial scales in Alberta rivers

Geneviève M. Carr, Patricia A. Chambers, and Antoine Morin

Abstract: The ability of land use to replace water quality variables in predictive models of periphyton chlorophyll *a* was tested with a 21-year data set for Alberta rivers. Nutrients (total dissolved P and NO_2 + NO_3) explained 23%–24% of the variability in seasonal chlorophyll *a*, whereas land use (human population density) explained 25%–28% of the variability. The best models included the combination of total dissolved P and population density, explaining 32%–34% of periphyton chlorophyll *a* variability. However, analysis of variance of chlorophyll *a* by ecoregions and ecozones explained about as much variability (28%–30%), and the inclusion of an ecoregion term into the regression models showed a diminished importance of land use as a predictor of chlorophyll *a*, with best models based on the combination of nutrients and ecoregion and explaining up to 43%–44% of periphyton chlorophyll *a* variability. Within ecoregions, land use was sometimes a good surrogate for nutrient data in predicting chlorophyll *a* concentrations. Overall, land use is a suitable surrogate for nutrients in regression models for chlorophyll *a*, but its inclusion in general models may reflect regional differences in nutrient–chlorophyll relationships rather than true land use effects on chlorophyll *a*.

Résumé : Une banque de données prises sur 21 années dans des rivières de l'Alberta nous a servi à vérifier la possibilité de nous servir de données d'utilisation des terres au lieu des variables de qualité de l'eau dans des modélisations de la chlorophylle *a* du périphyton. Les nutriments (P total dissous et NO_2 + NO_3) expliquent 23–24 % de la variabilité saisonnière de la chlorophylle *a*, alors que l'utilisation des terres (densité de la population humaine) explique 25–28 % de cette même variabilité. Les meilleurs modèles qui combinent P total dissous et la densité de population expliquent 32–34 % de la variabilité de la chlorophylle a du périphyton. Cependant, une analyse de variance de la chlorophylle *a* en fonction des écorégions et des écozones explique presque autant de variation (28–30 %); l'insertion d'une variable d'écorégion dans les modèles de régression fait diminuer l'importance de l'utilisation des terres comme facteur de prédiction de la chlorophylle *a*; les meilleurs modèles basés sur une combinaison des nutriments et des écorégions expliquent jusqu'à 43–44 % de la variabilité de la chlorophylle *a* du périphyton. À l'intérieur d'une écorégion, l'utilisation des terres est quelquefois une variable de rechange adéquate pour les données sur les nutriments pour prédire les concentrations de chlorophylle *a*. Somme toute, l'utilisation des terres peut servir adéquatement de variable de rechange pour les nutriments dans les modèles de régression de la chlorophylle *a*, mais son insertion dans les modèles généraux peut refléter les différences régionales dans les rapports nutriments-chlorophylle, plutôt que les véritables effets de l'utilisation des terres sur la chlorophylle *a*.

[Traduit par la Rédaction]

Introduction

Periphyton communities are often the dominant primary producers in rivers and streams, and shifts in their composition and abundance are known to have impacts that reverberate through higher trophic levels within individual ecosystems. However, the development of robust models that predict abundance of periphyton chlorophyll *a* on the basis of water quality in lotic ecosystems has lagged behind the development of similar models for planktonic chlorophyll *a* in lakes (e.g., Dillon and Rigler 1974). Dodds et al. (2002) recently published general models based on total N (TN) and total P (TP) concentrations in temperate streams that explained ~40% of the variance in both mean and maximum periphyton chlorophyll *a*. The authors' models contrast with phytoplankton models for lakes that often yield coefficients of determination >90% (Dillon and Rigler 1974). The lack of predictability in periphyton models has generally been attributed to high variability in periphyton communities owing, in large part, to patchiness in the communities caused by the heterogeneous nature of benthic environments in lake and, in particular, river ecosystems.

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There is clear evidence that periphyton abundance is often controlled by nutrient concentrations. Abundant growths of periphyton in nutrient-enriched areas have been documented (Welch et al. 1989) and nutrient-enrichment experiments have shown that periphyton can be P, N, or both N + P limited (Francoeur 2001). However, other factors have also been shown to influence periphyton abundance, including hydrologic disturbances that cause scouring of periphyton (Biggs 2000), invertebrate grazing of periphyton (Biggs et al. 1998; Anderson et al. 1999), and light availability (Bourassa and Cattaneo 2000). Empirical models that incorporate several of these factors have sometimes yielded higher coefficients of determination (e.g., Biggs 2000) than models based on nutrients alone, but the application of such models with multiple variables often becomes difficult because of a lack of data.

Several investigators have taken a different approach to predicting chlorophyll concentrations in lakes and rivers by relating chlorophyll *a* concentration at a station to land use within the drainage basin upstream of that station (Meeuwig and Peters 1996; Lohman and Jones 1999). Large temporal variability about true mean values makes it difficult to estimate seasonal average concentrations of nutrients precisely (Cattaneo and Prairie 1995) and land use variables may provide a better correlate of average nutrient concentrations than instream measurements. This is particularly true for forms of N and P that are considered bioavailable, such as inorganic N and soluble reactive P; these are notoriously difficult to estimate precisely and it is not clear that they truly represent bioavailable forms (Dodds 2003). Moreover, because nutrients that wash in from drainage basins may also be associated with factors such as contaminants and suspended particles, the biotic response to diffuse loading is most likely an integrated response to the cumulative effects of multiple stressors (Meeuwig and Peters 1996). Thus, the inclusion of land use variables into chlorophyll models may improve predictions by integrating the effect of more than one independent variable on periphyton biomass. This has been shown to be true for planktonic chlorophyll in lakes (Meeuwig and Peters 1996) and rivers (Lohman and Jones 1999).

Although land use has not been explicitly examined for periphyton at a broad scale, some investigators have recognized its possible effect. Dodds et al. (2002) reported correlation between periphyton chlorophyll *a* and percent urban and agricultural land use in a drainage basin but cautioned that anthropogenic effects could not be distinguished from natural geographic variation at the ecoregion level. Sabater et al. (2000) showed how land use and periphyton covary along a river system, whereas Biggs (1995) showed with a small data set that benthic chlorophyll *a* could be predicted by flood frequency, the proportion of the basin under high intensity agricultural use, and catchment geology. Munn et al. (2002) also showed that periphyton community composition varied with the amount of agriculture in the drainage basin.

The objective of this study was to assess the feasibility of using land use variables as surrogate predictors of periphyton chlorophyll *a* for rivers in Alberta, Canada, using a 21-year historical monitoring data set maintained by the Province of Alberta. Regression models based exclusively on either nutrients or land use were compared and then combined to determine the combination of variables that yielded the best predictive models. The effect of spatial scale (entire province versus ecozones and ecoregions) on modeling outcomes was also compared to evaluate the best scale for developing predictive models for periphyton chlorophyll *a* in rivers. Finally, general trends in chlorophyll–nutrient relationships at the provincial scale were compared with other published chlorophyll–nutrient models.

Methods

Study area

Alberta Environment measured periphyton chlorophyll *a* and water quality data at nearly 400 stations between 1980 and 2000 throughout the Province of Alberta. The frequency with which the stations were sampled varied: some stations were sampled at regular intervals (most often monthly), whereas others were sampled once or only occasionally. The 91 stations that were included in this study were chosen based on two main criteria. First, stations were chosen that had suitable replication of chlorophyll *a* measurements within a season. This decision was based on examination of average precision about the mean (determined as the standard error divided by the mean) and was an attempt to strike a balance between having high precision in estimates of seasonal means and having sufficient data for analysis. Thus, stations that had at least two replicate measurements of chlorophyll *a* in the spring and fall and three replicates in the summer were retained in this study. Average precision in seasonal mean chlorophyll *a* estimates retained in this study ranged from 20% to 28%. Seasons were defined according to the dominant discharge patterns in Alberta rivers such that spring corresponded to the months of April and May when discharge tends to be low owing to persistent cold temperatures in the headwaters. Summer corresponded to the months of June, July, and August when discharge tends to be high and variable owing to melting in the headwaters. Fall months were September and October, representing the period of freeze-up in the headwaters and generally low flows in the rivers.

The second criterion for inclusion of stations in the study was location of station at or near a watershed boundary, as delineated in the Prairie Farm Rehabilitation Administration Gross Watershed Boundaries for the Canadian Prairies (http://www.agr.gc.ca/pfra/main_e.htm). The Prairie Farm Rehabilitation Administration data set defines 879 drainage basins for Alberta and is the most complete data set available for drainage basins at the provincial level. This final selection yielded 91 stations, with a total of 447 seasonal mean or maximum observations. Stations were spread across seven major drainage basins in the province (Athabasca, North Saskatchewan, Red Deer, Bow, Oldman, South Saskatchewan, and Milk) and three of the five terrestrial ecozones (prairie: 67 stations, 28 observations; montane cordillera: six stations, 28 observations; boreal plains: 18 stations, 30 observations) as defined by Alberta Environmental Protection (1994). Because most of the available data were from the prairie ecozone, we examined the distribution of stations across three groups of ecoregions in the prairies (mixed and moist mixed grasslands: 25 stations, 132 observations; fes-

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cue grasslands: 25 stations, 171 observations; aspen parkland: 17 stations, 86 observations). Among the stations included in the analysis, the median number of years that a station was sampled was 1. Four stations on the Bow River were sampled for between 13 and 17 years and accounted for 100 of the total observations. The rest of the stations in the study were sampled for between 1 and 8 years (median = 1 year) during the 21-year study period with a median of two observations per year.

Water quality data

Monitoring data for water quality and benthic chlorophyll *a* in Alberta rivers were retrieved from the Alberta Environment surface water quality database (Edmonton, Alberta). Water quality variables included P (TP and total dissolved P (TDP)) and N (total Kjeldahl and NO_2 + NO_3). TN was determined by summing total Kjeldahl and NO_2 + NO_3. Ammonia was not included in analyses because it was at or below analytical detection limits ~45% of the time that it was measured. All other nutrient variables had values that fell below detection limits no more than 20% of the time that they were sampled. Measurements that fell below detection limits were replaced with one half the value of the detection limit. There was some variability in analytical methods over time and across laboratories for the water quality variables, but all methods approximately followed standard methods set out by the American Public Health Association (1998).

Land use data

Statistics Canada censuses of human population and agriculture from 1981, 1986, 1991, 1996, and 2001 were used to estimate human and animal population and land use practices on a census subdivision (CSD) basis across Alberta. Digital boundary files of CSDs for each census year were obtained from Statistics Canada through the Data Liberation Initiative. The number and density of individuals living within a drainage basin were determined from the census of human population. The agricultural censuses were used to determine the area of drainage basins under agricultural land (total farm area and total crop area) and the number of livestock units (cattle, swine, and poultry converted to livestock units based on manure production relative to an average beef cow of 450 kg; Ontario Ministry of Agriculture and Food 1998) within each basin.

Census maps were overlaid onto Alberta drainage basins to extract the subdivisions (or portions thereof) that fell within specific basins. Political boundaries rarely coincided with drainage basin boundaries, and so when a CSD overlapped a basin boundary, the percent CSD that fell within the basin was determined, assuming that the distribution of land use within the CSD was uniform. Land use in drainage basins in noncensus years was estimated as a weighted average of land use in the basins in census years before and after the sampling year.

Data analysis

Data were analysed with SYSTAT version 10 (Systat Software Inc., Richmond, California, http://www.systat.com). Where necessary, variables were $\log_{10}$-transformed to stabilize variance and normalize distribution of residuals. Seasonal mean chlorophyll *a* concentration was determined according to the criteria described above. Seasonal maximum chlorophyll *a* concentration was the highest average daily value for a station collected within any given season. Multiple regressions were used to explore relationships between seasonal mean and maximum epilithic chlorophyll *a*, water quality, and land use. Correlation among independent variables was assessed by examining Pearson correlation coefficients, and variables with significant (Bonferroni-adjusted $P < 0.05$) coefficients > 0.60 were entered into separate models. Multicollinearity among independent variables was further assessed by examining tolerance of each variable, equal to 1 minus the proportion of variance in each independent variable accounted for by all other independent variables. Low tolerance values (<0.50) indicated correlation among variables, in which case the models were rerun excluding at least one of the collinear variables. The multiple regression models that had the lowest residual mean square (RMS) were chosen as the best predictive models of dependent variables.

The influence of temporal autocorrelation on periphyton models was examined by comparing models that used the full data set with the same models that were run on a reduced data set that excluded the four stations that were sampled most frequently and most regularly over the study period. The reduced data set consisted of data from stations that were sampled infrequently (between 1 and 8 years of data per station) and irregularly over the study period and thus were unlikely to be temporally autocorrelated.

The influence of distribution of individual sampling stations across Alberta on relationships between periphyton chlorophyll *a* and nutrients and (or) land use was also evaluated by modeling chlorophyll *a* as a function of third-order polynomials of the latitude and longitude of each station (plus all possible interactions, leading to a total of 15 terms in the model) alone and in combination with nutrient and (or) land use predictors.

The effect of season (spring, summer, and fall) on periphyton chlorophyll *a* in Alberta rivers was evaluated by analysis of covariance (ANCOVA) with a seasonal term and all possible interactions entered into models that had nutrients and (or) land use as predictor variables (i.e., chlorophyll *a* = predictor + season + predictor × season, where predictor = nutrient and (or) land use predictor variables). A significant interaction between season and the predictor variables indicated a difference in slopes among seasons; a significant main effect of season indicated differences in the *y*-intercepts of the regression lines among seasons.

The influence of broad geographic patterns, at the scale of ecoregions and ecozones, on periphyton chlorophyll *a* was evaluated with ANCOVA by including a term that identified the ecoregion–ecozone in which a station fell, plus all possible interactions with other predictor variables, into regression models of chlorophyll *a* (i.e., chlorophyll *a* = predictor + ecoregion + predictor × ecoregion, where predictor = nutrient and (or) land use predictor variables). Differences in the proportion of variance explained (as determined by the coefficient of variation, r^2) with and without the factorial terms included in the models made it possible to evaluate the benefit of modeling chlorophyll *a* at different geographic scales of analysis.

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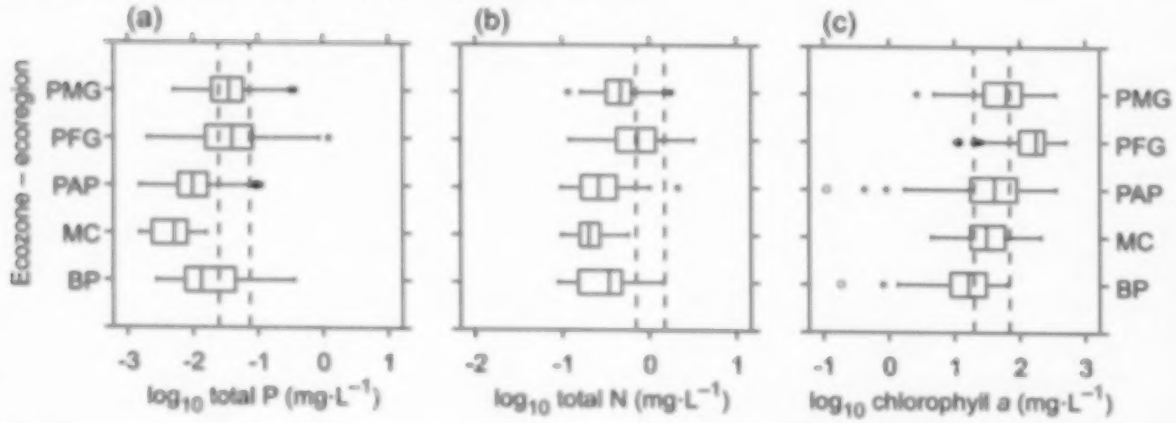
Table 1. Summary statistics of variables used in the analysis.

	Mean (SE)	Median	Minimum	Maximum	*n*
Epilithic chlorophyll *a* ($mg \cdot m^{-2}$)					
Mean	112 (5)	76.3	0.111	514	447
Maximum	165 (7)	121	0.152	988	447
TP ($mg \cdot L^{-1}$)	0.049 (0.005)	0.024	0.001	1.22	413
TDP ($mg \cdot L^{-1}$)	0.027 (0.003)	0.008	0.001	0.938	447
TN ($mg \cdot L^{-1}$)	0.575 (0.026)	0.416	0.089	3.31	340
$NO_2 + NO_3$ ($mg \cdot L^{-1}$)	0.255 (0.016)	0.069	0.001	1.63	447
Population density (individuals·km^{-2})	16.6	5.61	0.06	114	226
Livestock density (livestock units·km^{-2})	11.2	9.29	0.1	39.4	226
Farm land (% of basin)	41.6	48.5	0.1	98.0	226
Crop land (% of basin)	18.1	19.0	0.1	48.2	226
Basin area (km^2)	20 209	6489	1180	283 155	74

Note: Data are for all seasons, all years, and all stations. Land use data are averaged by drainage basin, not individual observations, since multiple observations may correspond to the same land use data. *n* is the number of observations; TP, total phosphorus; TDP, total dissolved phosphorus; TN, total nitrogen.

Fig. 1. Box-and-whisker plots of (*a* and *b*) nutrient ((*a*) total phosphorus (TP) and (*b*) total nitrogen (TN)) and (*c*) periphyton chlorophyll *a* concentrations in Alberta rivers, with observations separated by major terrestrial ecozone and ecoregion. MC corresponds to the montane cordillera ecozone and BP corresponds to the boreal plains ecozone. PMG, PFG, and PAP are located in the prairie ecozone and correspond to the mixed and moist mixed grassland ecoregions (PMG), the fescue grassland ecoregion (PFG), and the aspen parkland ecoregion (PAP), respectively. Broken lines represent oligomesotrophic (left broken line) and mesoeutrophic (right broken line) boundaries for TN, TP, and chlorophyll *a* proposed by Dodds et al. (1998).



Results

Chlorophyll and water quality

Periphyton chlorophyll *a* in Alberta rivers ranged from detection limits (0.1 $mg \cdot m^{-2}$) to >500 $mg \cdot m^{-2}$ and averaged ~100 $mg \cdot m^{-2}$ across the province (Table 1). Water quality in the rivers studied was, on average, oligotrophic with respect to TN and oligomesotrophic with respect to TP (Table 1; Fig. 1) according to the classification scheme proposed by Dodds et al. (1998). Chlorophyll *a* and nutrient concentrations differed among ecozones–ecoregions ($P < 0.001$, analysis of variance (ANOVA) with ecozone–ecoregion as the independent variable) such that mean chlorophyll *a*, TN, and TP were highest in the prairie fescue grassland ecoregion, although TP was similar in the fescue and in the mixed and moist mixed grassland ecoregions of the prairie ecozone. Periphyton chlorophyll *a* was lowest in the boreal plains ecozone, whereas TN and TP were lowest in the montane cordillera ecozone (Fig. 1).

Concentrations of periphyton chlorophyll *a* and TN were fairly stable over the study period, whereas TP declined throughout the 1980s (Fig. 2). However, chlorophyll *a* differed among seasons and tended to be highest in fall and equal and lower in spring and summer. Significant differences among seasons were also detected for nutrients ($P < 0.001$, ANOVA with season as the independent variable) such that nutrient concentrations were highest in spring and lowest in fall. The only exception to this seasonal nutrient trend was $NO_2 + NO_3$, which was higher in summer than in fall and differences among seasons were only marginally significant ($P = 0.01$, ANOVA with season as the independent variable) (Fig. 2).

Land use

The drainage basins examined in this study were large and ranged from 1180 – 283 155 km^2. Among these basins, human activity upon the landscape varied from intensively farmed agricultural areas (up to 98% of a drainage basin

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Fig. 2. Temporal patterns in (*a*) total phosphorus (TP) (mg·L^{-1}), (*b*) total nitrogen (TN) (mg·L^{-1}), and (*c*) periphyton chlorophyll *a* (mg·m^{-2}). Symbols are annual means ± 1 SE averaged across all stations. Curves are locally weighted regressions based on seasonal means: solid line, spring; dashed line, summer; dotted line, fall. Note the different scales on the *y* axes.

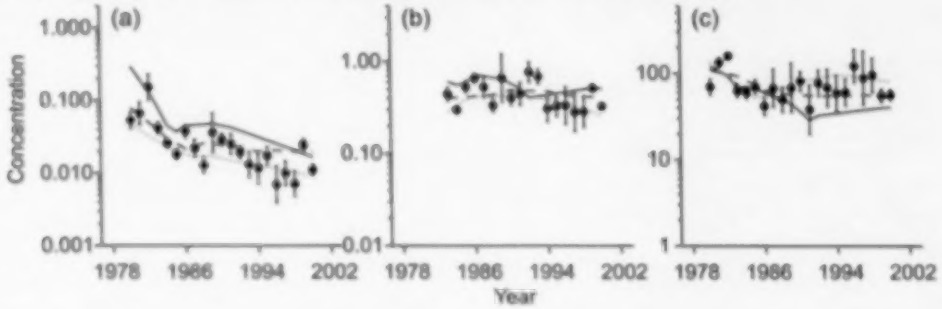
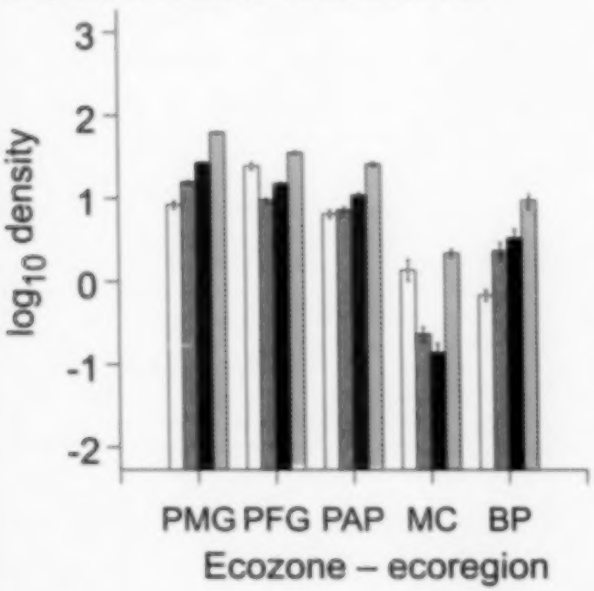


Fig. 3. Land use metrics across major ecozones and ecoregions in Alberta. Human density (open bars) is expressed as individuals per square kilometre and livestock densities (grey bars) are expressed as livestock units per square kilometre; proportion of land in crops (solid bars) and farms (hatched bars) are dimensionless. MC corresponds to the montane cordillera ecozone and BP corresponds to the boreal plains ecozone. PMG, PFG, and PAP are located in the prairie ecozone and correspond to the mixed and moist mixed grassland ecoregions (PMG), the fescue grassland ecoregion (PFG), and the aspen parkland ecoregion (PAP), respectively. Data are means ± 1 SE.



under farmland) to densely populated urban areas (114 individuals·km^{-2}) to drainage basins with almost no human activity (population and agricultural density estimates all very low) (Table 1). Human population density was greatest in the fescue grassland ecoregion (prairie ecozone) and lowest in the boreal plains ecozone of the province (Fig. 3). In contrast, agricultural activities, as measured by density of livestock and proportion of the drainage basin under crops or farmland, were all greatest in the mixed and moist mixed grassland ecoregions and lowest in the montane cordillera ecozone. Average human density exceeded livestock density in the montane cordillera ecozone and the fescue grassland ecoregion, whereas livestock density was greater than human density in the other three terrestrial regions. Significant proportions of variation in all measures of human activity upon the landscape (human and livestock population densities, proportion of basin in crop and farm land) were explained by terrestrial ecoregion following ANOVA for each variable with ecoregion as the dependent variable ($0.45 < r^2 < 0.78$, $P < 0.001$).

Riverine nutrient concentrations were significantly correlated with land use variables. In particular, estimates of P (TP and TDP) were positively correlated with estimates of agricultural activity (livestock density and proportion of basin in farm or crop land), whereas N variables (TN and NO_2 + NO_3) were better correlated with human population density (Table 2).

Multiple regression models

Provincial-scale models

Examination of the entire data set at a provincial scale, with no seasonal or geographic separation of the data, showed that the best water quality predictors of seasonal mean chlorophyll were the combination of concentrations of TDP and NO_2 + NO_3, explaining 23% of the variability in mean algal abundance (Table 3). Land use was a better predictor of chlorophyll *a* in Alberta rivers than water quality, explaining 28% of the variability in mean chlorophyll *a*. The best land use predictor of chlorophyll *a* at the provincial level was population density. The combination of water quality (TDP) and land use (population density) variables provided the best fit to the chlorophyll data at the scale of the entire province, explaining 34% of the variability in mean periphyton chlorophyll *a*. The same regression models performed on a reduced data set yielded virtually identical model coefficients with slightly higher RMSs and r^2 values that were between 3.4% and 5.3% less than those for the full data set (Table 3).

Models for maximum chlorophyll *a* did not differ considerably from those for mean chlorophyll *a*, although the nutrient-only model yielded slightly better predictions and the land use models yielded slightly worse predictions for maximum as compared with mean chlorophyll *a* (Table 3). The differences in r^2 between mean and maximum chlorophyll *a* models were on the order of only 0%–1% for

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Table 2. Pearson's correlation coefficient matrix of nutrient and land use variables.

	TP ($mg \cdot L^{-1}$)	TDP ($mg \cdot L^{-1}$)	TN ($mg \cdot L^{-1}$)	$NO_2 + NO_3$ ($mg \cdot L^{-1}$)
Basin area (km^2)	0.306	0.290	0.265	0.191
Population density (individuals·km^2)	0.107*	0.177	0.405	0.515
Livestock density (livestock units·km^2)	0.439	0.363	0.297	–0.141*
Farm land (% of basin)	0.482	0.402	0.349	–0.117*
Crop land (% of basin)	0.484	0.409	0.358	–0.104*

Note: All variables are $\log_{10}$-transformed. Correlation coefficients followed by an asterisk are not significant (Bonferroni-adjusted $P > 0.05$). Correlations are based on 340 records that are complete for all variables. TP, total phosphorus; TDP, total dissolved phosphorus; TN, total nitrogen.

nutrient-only models and 3%–4% for land use models. Similar to the mean chlorophyll models, models with the reduced data set yielded equivalent model coefficients and slightly higher RMSs and slightly lower r^2 values.

There was a spatial structure to the periphyton chlorophyll *a* data that was detected in multiple polynomial modeling of chlorophyll *a* as a function of the location (latitude and longitude) of sampling stations (Table 3). In general, periphyton chlorophyll *a* decreased from south to north and from east to west and location alone explained 33% and 32% of the variability in mean and maximum chlorophyll *a*, respectively. When geographic location was modeled in combination with nutrient and (or) land use predictor variables, a similar pattern emerged for both mean and maximum periphyton chlorophyll *a* as for when location was not taken into account. That is, the combination of nutrients (TDP) and land use (population density) explained the most variability (model $r^2 = 0.44–0.45$) in mean and maximum periphyton chlorophyll *a* when compared with land use or nutrient-only models. Nutrient and land use coefficients were similar between models that did and did not include the spatial component of sampling stations. Based on the consistency of modeling results for periphyton, in terms of regression coefficients for nutrients and (or) land use and patterns of variance explained among models that did and did not consider the spatial structure of the data, we elected to proceed with regression modeling without including spatial structure of the periphyton data.

A slight seasonal effect was also detected in periphyton chlorophyll *a* after taking into account the effects of nutrients and land use. Inclusion of an additional term to account for seasonal differences in the general models using the entire data set (Table 3, plus all possible interactions) yielded only modest improvements to the models (<2% increases in r^2), and exclusion of spring data yielded models with nonsignificant seasonal effects. ANCOVA to evaluate differences in slopes and intercepts in the general regression models detected significant differences for intercepts, but not slopes, of the continuous variables such that spring chlorophyll values were slightly lower ($P < 0.05$) than summer and fall chlorophyll values for any given unit (or combination thereof) of the independent variables in the regression model. Because the effects of season were small, we elected to ignore seasonal effects in subsequent modeling efforts.

Regional-scale models

Chlorophyll *a* varied significantly across ecoregions, and ecoregion alone explained approximately the same amount of variability in mean chlorophyll *a* as combined water quality and land use variables at the scale of the entire province (Table 4). Inclusion of ecoregion in the regression models as a categorical variable yielded considerable improvements in the amount of variation in chlorophyll *a* explained by the models. An additional 21.5% of the variability in mean chlorophyll was explained when ecoregion and all possible interactions between ecoregion and TDP and $NO_2 + NO_3$ were added to the nutrient-only model. The improvements to model fit conferred by land use at the provincial scale were essentially eliminated when the effect of ecoregion on chlorophyll–nutrient relationships was taken into account, resulting in the nutrient and ecoregion models being about as precise as the combined nutrient, land use, and ecoregions model (44.2% versus 45.4% of the variation in chlorophyll explained by the two models, respectively).

Similar patterns were observed for models of maximum chlorophyll *a* (Table 4). Ecoregions alone explained nearly 28% of the variability in chlorophyll *a*, and the inclusion of ecoregion and all possible interactions with nutrients, land use, or the combination of nutrients and land use yielded models that explained between 38% and 44% of the variability in maximum chlorophyll *a*. Similar to the case for mean chlorophyll *a*, the improvement in precision when nutrients and land use were modeled together at the provincial scale was essentially lost when ecoregion effects on maximum chlorophyll *a* were taken into account.

Significant two- and three-way interactions between ecoregion, nutrients, and land use precluded the possibility of developing a general predictive model for chlorophyll *a* (mean or maximum) based on water quality, land use, and ecoregion. To address the relationships at the ecoregion level, we ran individual multiple regressions for each ecoregion to identify the best models for predicting periphyton chlorophyll *a* concentrations based on water quality and (or) land use within a smaller area of the province. Because of the similarities in model results between mean and maximum chlorophyll *a* at the provincial level, we report here modeling efforts for regional effects on mean chlorophyll *a* only.

In general, models developed for individual ecoregions were similar in terms of the independent variables that were the best predictors of chlorophyll *a* (Table 5). Land use (population density or crop density) was a significant predictor of mean chlorophyll *a* in four of the five ecoregions examined, whereas dissolved nutrients (TDP and $NO_2 + NO_3$) were significant predictors in three of the five ecoregions. The combination of nutrients and land use yielded models

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Table 3. Comparison of regression models predicting seasonal mean and maximum periphyton chlorophyll *a* in Alberta rivers.

Predictor variable	Model No. and constraint	Model coefficient (SE) Constant	TDP ($mg \cdot L^{-1}$)	$NO_2 + NO_3$ ($mg \cdot L^{-1}$)	Population density ($individuals \cdot km^{-2}$)	RMS	r^2
Mean chlorophyll							
Nutrients	1. All data	2.58 (0.08)	0.28 (0.04)	0.17 (0.03)		0.234	0.227
	2. Reduced	2.49 (0.10)	0.27 (0.05)	0.13 (0.04)		0.259	0.174
	3. Spatial		0.18 (0.04)	0.12 (0.03)		0.186	0.401
Land use	4. All data	1.39 (0.04)			0.43 (0.03)	0.219	0.276
	5. Reduced	1.42 (0.04)			0.40 (0.04)	0.237	0.242
	6. Spatial				0.36 (0.05)	0.183	0.410
Nutrients and land use	7. All data	1.97 (0.10)	0.24 (0.04)		0.36 (0.03)	0.201	0.337
	8. Reduced	1.93 (0.11)	0.22 (0.04)		0.33 (0.04)	0.221	0.296
	9. Spatial		0.21 (0.04)		0.33 (0.04)	0.170	0.451
Latitude and longitude	10. Spatial					0.208	0.326
Maximum chlorophyll							
Nutrients	11. All data	2.77 (0.08)	0.29 (0.04)	0.16 (0.03)		0.224	0.239
	12. Reduced	2.68 (0.09)	0.28 (0.05)	0.13 (0.03)		0.252	0.186
	13. Spatial		0.19 (0.04)	0.12 (0.03)		0.180	0.405
Land use	14. All data	1.59 (0.04)			0.40 (0.03)	0.221	0.249
	15. Reduced	1.62 (0.04)			0.37 (0.04)	0.242	0.214
	16. Spatial				0.32 (0.05)	0.185	0.388
Nutrients and land use	17. All data	2.22 (0.10)	0.27 (0.04)		0.32 (0.03)	0.200	0.323
	18. Reduced	2.18 (0.11)	0.24 (0.04)		0.30 (0.04)	0.223	0.280
	19. Spatial		0.23 (0.04)		0.29 (0.04)	0.170	0.437
Latitude and longitude	20. Spatial					0.205	0.320

Note: Coefficients of nutrient and (or) land use terms and regression statistics (residual mean square (RMS) and r^2) for each category of predictor variables are shown for all data (447 observations), for a reduced data set that excludes the four most frequently sampled stations (347 observations), and for models based on the entire data set that include third-order polynomial terms (plus all interactions, for a total of 15 model terms) to describe location (latitude and longitude, in decimal degrees) of each sampling station. Regression statistics for models based solely on the third-order polynomial terms to describe location are also shown. Chlorophyll, nutrient, and land use variables were $\log_{10}$-transformed. TDP, total dissolved phosphorus.

with lower RMSs (and therefore higher precision) than province-wide models in the fescue grassland ecoregion of the prairies and the montane cordillera ecozone. Models for the other three ecoregions, based only on either land use or nutrients, had RMSs that were higher than or equal to province-wide models and lower coefficients of determination. Caution should be used in interpreting results of the montane cordillera and boreal parkland ecozone models, since sample sizes in these groups were small (n = 28 and 30, respectively).

Discussion

Models for prediction of mean and maximum chlorophyll *a* in rivers in the Province of Alberta, Canada, were best when based on a combination of nutrients (TDP) and land use (population density). However, when the effects of ecoregion on chlorophyll *a* were taken into account, nutrient-only models explained more variability than land use models and about equal amounts of variability in models that combined nutrients, land use, and ecoregion for the entire province. Biggs (1995) also showed that agricultural land use in conjunction with bedrock geology and frequency of floods were good surrogates for nutrient data in predicting chlorophyll *a* concentration. Similarly, Dodds et al. (2002) reported that mean chlorophyll was positively correlated with land use metrics, such as percent urban, crop, and pasture lands, and drainage area. However, neither of the above studies explicitly compared regression models developed with nutrients with those developed with land use, as we have done here.

The fact that predictions of chlorophyll *a* based on land use were about as good as, or better than, predictions based solely on nutrients is notable, especially given the fact that estimates of land use in Alberta were relatively coarse when compared with the more intensively collected water quality data. Although satellite imagery may have improved estimates of land use for Alberta, census data are readily available, inexpensive, and updated every 5 years (in Canada) and this makes them appealing as a means to derive rough predictions of how much benthic chlorophyll *a* can be expected in any one location.

Human population density, which was the best overall land use predictor of chlorophyll *a* at the provincial level, was well correlated with $NO_2 + NO_3$ concentrations, whereas agricultural activities were well correlated with P concentrations. These patterns were consistent with human activities upon the Alberta landscape. First, efforts to curb eutrophication through P reductions have led to general increases in the N:P ratio of sewage to and situations where N, but not P, tends to be found in high concentrations in effluents from many municipal wastewater treatment plants (Chambers et al. 1997). Thus, in areas where human population density is high in Alberta, N concentrations also tend to be high. In agricultural landscapes in Alberta, the application of livestock manure as fertilizer to cropland has, until recently, been done to meet plant N requirements. However,

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Table 4. Variance partitioning among general linear models for mean and maximum chlorophyll *a* in Alberta rivers.

Model	RMS	r^2
Mean chlorophyll		
Ecoregions only (ANOVA model)	0.213	0.301
Nutrients only (model 1)	0.234	0.227
Nutrients and ecoregions (full model)	0.176	0.442
Land use (model 4)	0.219	0.276
Land use and ecoregions (full model)	0.183	0.406
Nutrients and land use (model 7)	0.201	0.337
Nutrients, land use, and ecoregions (full model)	0.172	0.454
Maximum chlorophyll		
Ecoregions (ANOVA model)	0.214	0.278
Nutrients only (model 11)	0.224	0.239
Nutrients and ecoregions (full model)	0.175	0.429
Land use (model 14)	0.221	0.249
Land use and ecoregions (full model)	0.187	0.377
Nutrients and land use (model 17)	0.200	0.323
Nutrients, land use, and ecoregions (full model)	0.171	0.443

Note: Model numbers refer to the models in Table 3 based on the full data set (447 observations). "Full model" is the combination of the model terms from Table 3 plus an ecoregion term and all possible interaction. All variables are $\log_{10}$-transformed. RMS, residual mean square of the models.

because N:P in manure is low (~ 5:1; US Department of Agriculture 1992) relative to plant requirements (15:1), there has tended to be an overapplication of P on the landscape. The excess P could then potentially move into surface waters, leading to a correlation between agricultural land use and P concentrations. Modeling results for chlorophyll *a* reflected the correlations between land use and water chemistry: when more than one variable was included in a model, these consisted of a form of P or a land use variable that was correlated with P (i.e., livestock, farm, or crop density) and a form of N or a land use variable correlated with N (i.e., human population density).

The fact that inclusion of an ecoregion term into the general province-wide nutrient models yielded as good predictions as models that combined land use, nutrients, and ecoregions suggests that the improvements in models when land use, but not ecoregion, was included were probably due to a covariance between ecoregion and land use. Land use patterns did vary significantly among ecoregions in this study: population density was greatest in the fescue grassland ecoregion, agricultural activity was greatest in the mixed and moist mixed grassland and aspen parkland ecoregions, and human activities were generally low in the boreal plains and montane cordillera ecoregions. These patterns are not surprising, as some ecoregions will naturally be more readily inhabited than others (Smith et al. 2003).

Spatial patterns in the Alberta data set were also detected when periphyton chlorophyll was modeled as a function of geographic location of sampling stations: periphyton biomass was, on average, highest in the southern and eastern portions of the province, corresponding to areas of high agricultural activity and warmer climates. However, taking into account the spatial structure of the data did not eliminate relationships between chlorophyll and nutrients and (or) land use. In fact, models that included both the spatial component of the data and nutrients and (or) land use as predictor variables had coefficients for the nutrient and land use variables that were very similar to those of models that did not include location of sampling stations.

Dodds et al. (2002) cautioned against the ecoregion modeling approach because of the problems of covariance between water quality, land use, and ecoregion and the general lack of suitably pristine reference stations within some ecoregions. However, it is our opinion that, in the presence of correlations between land use and ecoregion, the question becomes one of whether predictive models can be enhanced by looking at chlorophyll–nutrient (or land use) relationships within an ecoregion rather than across many ecoregions. In our study, land use was well-correlated with chlorophyll *a* within some ecoregions and estimates of anthropogenic activities (human density and proportion of basin under crops) yielded the best models for chlorophyll *a* in the mixed and moist mixed grassland and aspen parkland ecoregions and the combined effects of land use and nutrients yielded best models for chlorophyll in the fescue grassland and montane cordillera ecoregions. These patterns support the hypothesis that land use can be a good surrogate for nutrient data in predicting periphyton chlorophyll *a* concentrations. Although we advocate the ecoregion modeling approach in this study, we acknowledge that caution must be exercised when interpreting results from one ecoregion and applying these to another ecoregion that may have very different chlorophyll – nutrient – land use patterns.

Many published chlorophyll–nutrient models rely on total rather than dissolved forms of nutrients. Although dissolved nutrients may not be ideal for indicating nutrient status of surface waters because of high sampling variability and rapid turnover (Dodds 2003), their use in empirical modeling exercises is justified, since they are usually highly correlated with total forms of the same nutrients. In the case of the Alberta data set, total and dissolved forms of P and N were well correlated on a logarithmic scale (Pearson's r = 0.84 and 0.55 for P and N forms, respectively) and there were more observations of dissolved nutrients available for

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Table 5. Regional models of mean periphyton chlorophyll *a* based on water quality, land use, or the combination of water quality and land use.

Region	Equation	RMS	r^2
Fescue grasslands (prairie ecozone)	1.93 (0.09) + 0.11 (0.03) × TDP + 0.31 (0.04) × population density	0.083	0.296
Mixed and moist mixed grasslands (prairie ecozone)	1.44 (0.08) + 0.31 (0.07) × population density	0.170	0.125
Aspen parkland (prairie ecozone)	0.65 (0.21) + 0.86 (0.19) × crop land	0.296	0.197
Montane cordillera ecozone	4.09 (0.68) + 1.00 (0.26) × TDP + 0.34 (0.10) × population density	0.095	0.398
Boreal plains ecozone	1.86 (0.35) + 0.49 (0.21) × NO_2 + NO_3	0.262	0.156

Note: All variables were $\log_{10}$-transformed. Values in parentheses are SEs. TDP, total dissolved phosphorus; RMS, residual mean square. Units are according to Table 1.

modeling, thereby increasing statistical power by increasing sample size.

TN and TP were also significant predictors of periphyton chlorophyll *a* in this study at the scale of the entire province (Table 6), but the best models based on total nutrients had lower r^2 and higher RMSs than those based on dissolved forms of the nutrients. We compared models based on TN and TP developed with the Alberta data with models published by Dodds et al. (2002) for a literature data set consisting mostly of sites in North America and New Zealand and found that in all cases, the coefficients of the models developed with Alberta data were significantly different from those of the published models. In general, models with Alberta data had slightly higher intercepts (indicating, on average, more chlorophyll per unit nutrient in Alberta rivers) and slightly shallower slopes such that published models tended to underpredict chlorophyll in Alberta rivers (Fig. 4). However, the coefficients for the slopes for the TN models in particular are quite close (0.63 for Alberta versus 0.72 for published data), suggesting a generality in chlorophyll–nutrient relationships that requires only minor adjustment for different regions.

Our results indicate that scale of analysis impacts the predictability of chlorophyll models and there are several lines of evidence within the data examined to support this conclusion. Although there was good correspondence between the province-wide models developed here and other, published models for temperate streams, the predictability of these models was weak. In the case of the Alberta data, a simple ANOVA on chlorophyll among ecoregions explained as much variability as the more complex multiple regression models at the scale of the province. Thus, for the province as a whole, it is possible to get as good a prediction for chlorophyll at a station simply by knowing in which ecoregion it falls as it is by knowing land use characteristics of the drainage basin or instream nutrient concentrations. However, the inclusion of a term to account for ecoregion into the regression models as well as multiple regression analysis on ecoregion subsets of the data showed improvements in terms of modeling capacity for chlorophyll *a*. At the provincial level, models for mean and maximum chlorophyll *a* explained between 37% and 45% of the variability based on different combinations of independent variables, and within individual ecoregions, reductions in RMSs and improvements in r^2 values, relative to the province-wide models, were detected. The empirical models developed here for ecoregions could be used as reference points for the development of predictive models for chlorophyll that are more specific to the different regions of the province: in some cases, this might imply a more detailed land use analysis within an ecoregion, and in others, it might imply the gathering of more specific water quality data.

Although an understanding of the factors that control periphyton abundance is important from an ecological perspective, these same factors make implementation of general models for periphyton difficult, from a management perspective: it is uncommon that all factors needed to predict chlorophyll *a* are measured in routine monitoring programs, leaving predictions of chlorophyll *a* subject to considerable uncertainty. The issue of predictability based on regression models is not a new one and, in fact, has been a key criti-

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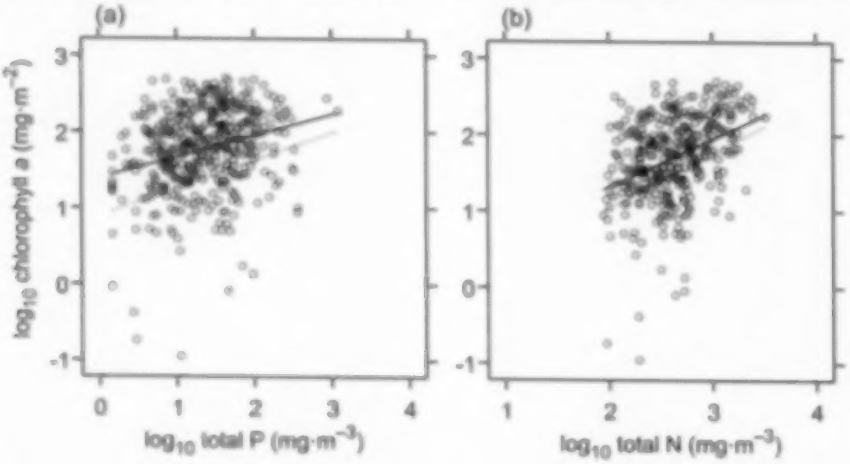
Table 6. Comparison of models that predict mean periphyton chlorophyll *a* based on total nitrogen (TN) and total phosphorus (TP) for Alberta data and for a literature data set published by Dodds et al. (2002).

Data source	Model	*n*	r^2	RMS	Significance test	
					$F_{[df1,df2]}$	*P*
TN models						
Dodds et al. 2002	−0.40 + 0.72(TN)	198	0.30	0.215		
Alberta	0.06 + 0.63(TN)	340	0.14	0.282		
H_0: coefficients = 0					$1790_{[2,338]}$	<0.001
H_0: coefficients = Dodds et al. 2002					$28.9_{[2,338]}$	<0.001
TP models						
Dodds et al. 2002	0.89 + 0.37(TP)	254	0.13	0.260		
Alberta	1.39 + 0.28(TP)	413	0.07	0.287		
H_0: coefficients = 0					$2274_{[2,411]}$	<0.001
H_0: coefficients = Dodds et al. 2002					$104.4_{[2,411]}$	<0.001
TN + TP models						
Dodds et al. 2002	−0.41 + 0.59(TN) + 0.20(TP)	193	0.38	0.184		
Alberta	−0.03 + 0.70(TN) − 0.08(TP)	340	0.14	0.282		
H_0: coefficients = 0					$1194_{[3,337]}$	<0.001
H_0: coefficients = Dodds et al. 2002					$44.9_{[3,337]}$	<0.001

Note: Slight variations from published models reflect corrections made to models after publication (W.K. Dodds, Biology, Kansas State University, Manhattan, KS 66506, USA, personal communication). Chlorophyll *a*, TN, and TP were $\log_{10}$-transformed in all models. Chlorophyll *a* is expressed as $mg \cdot m^{-2}$; TN and TP are expressed as $mg \cdot m^{-3}$. RMS, residual mean square of the models. Two tests of significance for regression models with Alberta data are shown: a test of the hypothesis of no difference from zero for all coefficients, including the intercept (H_0: coefficients = 0), and a test of the extrinsic hypothesis of no difference to the models of Dodds et al. (2002) (H_0: coefficients = Dodds et al. 2002). Models for Alberta include data from all seasons and all stations in the province (i.e., no geographic limitation on selection of data, as explained in the Methods).

Fig. 4. Relationship between periphyton chlorophyll *a* and (*a*) total phosphorus (TP) and (*b*) total nitrogen (TN) in Alberta rivers. Solid lines correspond to chlorophyll–nutrient models fit with Alberta data; broken lines are regression models of Dodds et al. (2002).



cism of empirical regression models for chlorophyll, even in lakes (Prairie 1996). The results of this study indicate that estimates of land use are about equal to those of nutrients in terms of their predictive capabilities for periphyton chlorophyll in Alberta rivers. The implications of these observations are that monitoring water quality in the hopes of predicting periphyton abundance is somewhat futile. If the goal of the monitoring program is to ultimately manage periphyton chlorophyll, management authorities would be wise to expend resources in localized areas and focus on collecting land use and water quality data specific to the region rather than looking for broad patterns. Over a broad geographic area, land use estimates will do as suitable a job as nutrients in predicting chlorophyll concentration in a river, and probably at considerably less expense.

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Interactions of productivity, predation risk, and fishing effort in the efficacy of marine protected areas for the central Pacific

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Abstract: Ecospace biomass-dynamics models for the central North Pacific predict strong space-time variation in abundances of various trophic groups in relation to nutrient-driven patterns in primary production and circulation-driven concentration of production in convergence areas. The model predicts simple patterns in ecosystem organization and abundances along productivity gradients. Predicted patterns are robust to alternative assumptions about how mobile organisms may alter dispersal behavior in relation to local fitness (per capita gain from net food intake minus predation mortality). Large marine protected areas (MPAs) would be needed to rebuild endangered populations and counter impacts of growing fishing effort. We expected that increases in dispersal rate in response to lower food availability and higher predation risk would reduce efficacy of MPAs as a management tool. Instead, simulations indicated that this negative effect may generally be eliminated or even reversed by positive effects of fitness-maximizing behaviors. Interannual variability in ocean circulation can further reduce the efficacy of MPAs; therefore, the dynamic nature of pelagic environments should also be considered in MPA design. Anomalies in ocean circulation may shift productive areas relative to MPA location, resulting in increased fishing mortality and (or) misinterpretation of catch statistics.

Résumé : Des modèles Ecospace de dynamique de la biomasse du centre du Pacifique Nord prédisent une forte variation spatio-temporelle de l'abondance de divers groupes trophiques dans les zones de convergence en réaction aux patrons de production primaire contrôlés par les nutriments et à la concentration de la production contrôlée par la circulation. Le modèle prédit des patrons simples d'abondances et d'organisation de l'écosystème le long de gradients de productivité. Les patrons prédits sont robustes par comparaison aux présuppositions de rechange concernant la manière dont les organismes mobiles peuvent changer leur comportement de dispersion en fonction de la fitness locale (gain individuel dérivé de l'ingestion nette de nourriture moins la mortalité due à la prédation). Il faudrait de grandes zones de protection marine (MPA) pour reconstituer les populations menacées et résister aux efforts croissants de la pêche commerciale. Nous nous attendions à ce que des augmentations du taux de dispersion en réaction à la baisse de disponibilité de nourriture et à l'accroissement du risque de prédation viennent réduire l'efficacité des MPA comme outils d'aménagement. Au contraire, les simulations indiquent que cet effet négatif serait généralement éliminé ou même renversé par les effets positifs des comportements visant à maximiser la fitness. La variabilité d'une année à l'autre de la circulation océanique peut réduire encore plus l'efficacité des MPA; il faut donc tenir compte de la nature dynamique des environnements pélagiques lors de la planification des MPA. Des anomalies dans la circulation océanique peut déplacer les zones productives par rapport à la position des MPA, ce qui entraînera une augmentation de la mortalité due à la pêche et (ou) une interprétation erronée des statistiques de récolte.

[Traduit par la Rédaction]

Introduction

The idea of using closed areas, reserves, or marine protected areas (MPAs) for rebuilding and (or) conserving fish stocks dates back as early as Garstang (1900). The use of models for evaluating the utility of closed areas on yield per recruit extends back to the early work of Beverton and Holt (1957), and recent elaborations of these models have seen growing use (Guenette et al. 1998; Russ and Alcala 1996). One of the key issues in examining the consequences of spa-

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tial policies has been the dispersal rate across closed area boundaries; high dispersal rates reduce the efficacy of MPAs. This is expected to be a particularly serious limitation of MPAs for the conservation of pelagic fishes, which are of special concern today (Myers and Worm 2003). There has been growing pressure in the recent decade to adopt marine reserves (or MPAs) as a management tool for commercial fisheries. The basic idea is to limit fishing mortality rate by restricting the spatial distribution of fishing effort to some fraction of the stock distribution (Walters 2000).

Analytical explorations of the efficacy of MPAs rarely consider other well-known ecological and behavioral processes that might diminish the effectiveness of MPAs. Many models assume passive, random diffusion of fish between protected and nonprotected areas; yet a considerable body of research points to the fitness-optimizing nature of animal movement that deviates quite strongly from random diffusion (e.g., Charnov 1976; Stephens and Krebs 1986). In this paper, we define fitness as the difference between productivity and predation risk, or total production minus total consumption. A concern in modeling spatial patterns of interactions is how active, fitness-maximizing behaviors might affect policy outcomes. Moreover, evaluations of MPAs that consider indirect effects through trophic interactions suggest diminished benefits for fisheries (Walters et al. 1999).

Trophic effects and fitness-optimizing dispersal patterns are expected to be pronounced for prey species of higher trophic-level fishes (e.g., mahi mahi (*Coryphaena hippurus*), skipjack tuna (*Katsuwonus pelamis*), and the communities of epipelagic and mesopelagic fishes that are common in pelagic seas). As predation risk increases inside MPAs because of the buildup of large predators, prey may tend to increase dispersal rates across MPA boundaries to avoid high risk areas. These effects may ultimately be seen at higher trophic levels through two processes. Directed prey dispersal may reduce food availability for high trophic-level fishes, thereby reducing the productivity of closed areas. Because juveniles of high trophic-level fishes are also prey items for many fishes (e.g., juvenile yellowfin tuna, *Thunnus albacares*, are preyed upon by adult blue marlin, *Makaira nigricans*), recruitment rates to the adult pool in closed areas might be diminished through active dispersal of juveniles that may be vulnerable to bycatch or directed fisheries outside of the closed area (Essington 2001).

The productivity of the closed area, an obvious factor in determining MPA siting, depends on a suite of oceanographic processes that are dynamic over space and time. This is especially true for large pelagic ecosystems, where productivity is dictated by seasonal and annual fluctuations in major current patterns (e.g., Fiedler and Bernard 1987; Polovina et al. 2001). It is not at all clear whether a spatially fixed, closed area can be effective in a pelagic ecosystem. Siting locations of MPAs is a question of management objectives and goals relative to the distribution of endangered species as well as periodic oceanographic features that tend to attract fish over time (e.g., Seki et al. 2002). For example, seasonal closures have recently been implemented for central Pacific longline fisheries to reduce turtle bycatch (Ito and Machado 2001). These areas were selected based in part on historical catch rate data of turtles and recent satellite tracking information on turtles. The question still remains: are the temporary closed areas sufficient to meet management objectives? Are simple advection–diffusion movement models sufficient for predicting the outcome of such closed area policies? Since many large-scale pelagic fisheries rely on commercial catch rate data for monitoring, what idiosyncrasies might closed area policies introduce into data sets that are used for monitoring abundance?

Here, we use food web models to explore alternative spatial closure polices in the central North Pacific (CNP) ecosystem and explore the sensitivity of policy decisions to alternative representations of fish dispersal and the dynamics of oceanographic processes. This food web consists of a guild of apex predators including tunas (*Thunnus* spp.), billfishes (*Xiphias gladius* and *Makaira* spp.), and sharks (predominantly blue shark, *Prionace glauca*), all of which are captured in an international fleet of longline and purse seine fisheries.

Methods

This is the fourth in a series of Ecosim-based (Walters et al. 1997, 2000) ecosystem models for the CNP. The previous models (Kitchell et al. 2002; Cox et al. 2002*a*, 2002*b*) represent a progression of model complexity and improvements in parameter estimates. This version uses the parameter values (i.e., biomasses, total mortality rates, consumption rates, etc.) developed by Cox et al. (2002*b*) as the basis for a spatially dynamic version of trophic interactions mediated by differences in habitat productivity, predation risk, and fishing effort.

We explored alternative policy options using Ecospace, a spatially explicit ecosystem model that accounts for spatial distribution of fishing effort, trophic interactions, and population dynamics for a collection of species or pools within a defined region or area (Walters et al. 1999). Ecospace represents all biomass pools on each of a collection of spatial map cells, and simulates dispersal–migration–transport of biomass across cell boundaries. For the CNP, we were able to assemble information from satellite imagery and other spatial-modeling exercises (e.g., Lehodey et al. 1998) on patterns of primary production and water movement (surface current vectors) to provide realistic bottom-up forcing of production processes. Other species in the food web were then assumed to be impacted to varying degrees by physical transport processes (ranging from passive transport of plankton and zooplankton biomass to active and oriented movement by larger fishes). Alternative spatial policies were evaluated by comparing changes in simulated biomass and catches over a 50-year scenario, where we assume effective fishing effort will double by year 50.

Population dynamics and trophic interactions

Dynamics and trophic interactions in Ecospace are based on the same set of differential equations, and delay-difference equations used to represent trophic ontogenies for groups that are split into juvenile and adult biomass pools, which are used in Ecosim (Walters et al. 1997, 2000; Walters and Kitchell 2001). For aggregated biomass groups (B_i), temporal dynamics are described by

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$$(1)\qquad \frac{dB_i}{dt} = g_i\sum_j C_{ji} - \sum_j C_{ij} + I_i - (m_i + F_i + e_i)B_i$$

where g_i represents net growth efficiency; C_{ji} and C_{ij} are the consumption rate of group j by group i and the consumption of i by j, respectively; I_i is biomass immigration rate (from other cells); m_i is nonpredation mortality; F_i is fishing mortality; and e_i is biomass emigration rate (to other cells). For linked adult and juvenile groups, full age-structured difference equations were used in place of the differential equation to calculate monthly changes in juvenile numbers and biomass, and juveniles then recruit into the adult pool at a specific age. Monthly changes in biomass for adult groups were calculated using delay-difference equations (see Walters et al. 2000 for details).

The equations for change in consumption rates over time in Ecosim–Ecospace have an implied spatial representation for fine-scale spatial behaviors that can severely limit predation, such as shoaling or vertical migration or deliberately hiding from predators. The notion here is that individuals spend a majority of time hiding from predators (unavailable) and make periodic forays to restricted foraging arenas where they are vulnerable to predation (available). These processes occur at very short time and space scales (seconds to minutes, centimetres to metres), and the exchange process between available and unavailable states occurs rapidly in comparison with changes in biomass, so that we can approximate time-varying consumption with an equilibrium solution at each B_i–B_j state (Walters and Juanes 1993). This model implies that consumption of i by j is limited to how fast prey exchange between available and unavailable states (v_{ij} and v'_{ij}). The consumption rate equation that represents these fine-scale movement – behavior dynamics is

$$(2)\qquad C_{ij} = \frac{a_{ij}v_{ij}B_iB_j}{v_{ij} + v'_{ij} + a_{ij}B_i}$$

where a_{ij} is the effective rate of search for prey that are in vulnerable state at any moment, and v_{ij} and v'_{ij} are the behavioral exchange rate parameters for moving from available to unavailable states, respectively. The effective rate of search is calculated by solving eq. (2) for a_{ij}, specifying values of v_{ij} and assuming base consumption rates ($C_{ij,0}$, $B_{i,0}$, and $B_{j,0}$) from initial input parameters and Ecopath mass balance estimates. The vulnerability parameters (v_{ij}) specify the upper limit of predation mortality, thus v_{ij} is simply a ratio of maximum predation mortality to base predation mortality (i.e., $v_{ij} = k_{ij}\,C_{ij,0}/B_{i,0}$, where $k_{ij}(1, \infty)$). Low k_{ij} values ($k_{ij} < 2$) imply donor-control predation mortality, whereas high values imply mass-action or top-down control.

Movement among spatial cells

Ecospace calculations involving eqs. 1 and 2 (and the more complex age-structured dynamics) are carried out for individual map cells referenced by rows (r) and columns (c). Instantaneous movement rates across cell boundaries (e_i in eq. 1) are a function of average annual movement distances. Estimates of these annual distances for model groups are provided (Table 1). The e_i terms in eq. 1 consist of a density-independent dispersal plus advection flow $(M_i + V_i)B_i$ across each spatial cell face that is not at the grid boundary (we assume densities outside the grid are equal to densities at grid boundary at each time step) or adjacent to a land cell. The instantaneous dispersal–diffusion rates M_i are assumed proportional to mean annual movement distance for each species or biomass type. Instantaneous advection rates V_i are calculated from current fields. The immigration rate terms I_i consist of similar $(M_i + V_i)B_i$ input rates proportional to abundances in surrounding cells.

Instantaneous movement rates M_i are calculated from swimming speeds S_i by estimating the proportion of B_i that could exit each cell boundary per unit time (i.e., that start time step dt within a band of width $S_i\,dt$) and would exit the cell if movement orientation over time dt is random. This geometric argument results in the prediction $M_i = S_i/\pi L$, where L is the length of a grid cell side (100 km for this study). For some fishes like tunas, we were able to correct the M_i by using direct information on dispersal rates from field tagging programs; typically such data indicate considerably lower dispersal rates than would be predicted from swimming speed alone.

M_i can be set to cause relatively higher e_i from "unsuitable" habitats. Instantaneous M_i rates across cell boundaries were adjusted upward by a multiplicative factor (see Table 1) for cells defined as unsuitable habitat for group i. For animals in unsuitable habitat cells within five grid cells of suitable habitat, emigration rates were distorted such that movement was more oriented towards preferred habitat (M values for cell sides facing good habitat cell(s) increased, M values for cell sides facing away from good habitats decreased). This assumes that organisms can detect habitat gradients within each monthly time step (i.e., small random displacements from their present position are not explicitly modeled, just the mean displacement in a preferred direction based on cumulative information gained over each monthly time step) for at least some distance when then they find themselves in unsuitable areas.

To consider more complex movement of species in space, we developed two alternative movement models where M_i vary according to relative values of fitness. M_i increase in areas of low fitness and decrease in areas of high fitness. Note that an increase or decrease in M_i does not imply a change in S_i; but rather, a reduction in M_i implies an increase in turning frequency such that the animal is more likely to remain in the cell. Both of these fitness-optimized movement models are based on the idea that animals will move to maximize their productivity and minimize their predation risk. We refer to the difference between productivity and predation risk as fitness, recognizing that a rich literature exists that derives alternative representations of fitness-maximizing rules based on detailed considerations of species life histories (e.g., Smith 1982; Stephens and Krebs 1986). Based on our definition of fitness, we calculated a fitness measure for each species i within each Ecospace cell as

$$(3)\qquad f_i = \frac{g_i\sum_j C_{ij} - \sum_j C_{ji}}{P_i}$$

where $g_i\sum_j C_{ij}$ represents gains from consumption, $\sum_j C_{ji}$ represents losses to predation, and P_i is the density of species i. Equation 3 is calculated for each spatial cell at each time

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Table 1. Dispersal rate parameters and habitat preferences for species or groups in the Ecospace model.

		Movement parameters				Habitat associations		
Group	Group code	Base dispersal rate (km·year^{-1})	Relative dispersal in unsuitable habitat	Relative vulnerability to predation in unsuitable habitat	Relative feeding rate in unsuitable habitat	All habitats	Warm water	Cool water
Large bigeye	lBE	3000	2	2	0.60	+		
Small bigeye	sBE	2000	1.2	3	0.60		+	
Large yellowfin	lYF	3000	2	2	0.01	+		
Small yellowfin	sYF	2000	1.2	2	0.01		+	
Large albacore	lAB	4000	3	2	0.01	+		
Small albacore	sAB	2000	3	2	0.01			+
Large blue shark	lBS	1000	2	2	0.01	+		
Small blue shark	sBS	500	2	2	0.01			+
Blue marlin	BM	3500	1.2	2	0.50		+	
Large sharks	lS	500	2	2	0.01	+		
Brown sharks	BS	500	2	2	0.01	+		
Swordfish	SRD	2000	2	2	0.01	+		
Other billfish	oBF	500	2	2	0.01	+		
Mahi mahi	MM	300	3	2	0.01	+		
Small scombrids	SS	300	3	2	0.01		+	
Flying squid	FS	500	2	3	0.30			+
Skipjack	SJ	300	3	2	0.01	+		
Large leatherback	lLB	300	2	2	0.01	+		
Small leatherback	sLB	300	2	2	0.01	+		
Large loggerhead	lLH	1000	2	2	0.01			+
Small loggerhead	sLH	300	2	2	0.01			+
Jellyfish	JF	300	1.1	2	0.01	+		
Lance	L	300	2	2	0.01	+		
Squids	S	300	2	2	0.01	+		
Flying fishes	FF	300	3	2	0.01	+		
Meso fish nekton	MFN	300	3	2	0.01	+		
Epi fish nekton	EFN	300	3	2	0.01	+		
Epi micronekton	EMN	100	3	2	0.01	+		
Meso micronekton	MMN	100	1.1	2	0.01	+		
Phytoplankton	PP	100	1.1	2	0.01	+		
Detritus	D	300	1.1	2	0.01	+		

Note: Unsuitable habitat refers to areas where the species is not normally found and is defined by the Ecospace user for each species.

step to produce a set of relative fitness gradients for each species or group in the model, and these f_i values ultimately define cell-specific M_i.

Based on this relative measure of fitness, we constructed two alternative movement models in Ecospace: (*i*) a variable emigration rate model (VE) and (*ii*) a directed movement model (DM). For both models, we assume that relative movement rates (H_i) decrease in cells with high fitness and increases to a maximum of two times the base movement rate in cells of low fitness. Specifically, the relative movement rate of species i is related to local fitness by

$$H_i = \frac{2e^{-k_i f_i}}{1 + e^{-k_i f_i}} \quad (4)$$

where $k_i = \ln(9)/(\rho Z_{0,i})$; ρ are scaling parameters; $Z_{0,i}$ represents base natural mortality rate in suitable habitat, with no fishing; and the maximum possible movement rate relative to base M_i is 2. Here k_i scales the relationship between movement rate and fitness, such that 90% of the total possible emigration is reached when $f_i = \rho Z_{0,i}$. At each time step, M_i (listed in Table 1) are multiplied by H_i to rescale annual M_i based on relative fitness values (f_i). Examples of relative e_i are shown for f_i in the range (–15, 15) (Fig. 1). The plots are given for instantaneous mortality rates of $Z = 0.5$ and $Z = 0.15$ and a range of ρ. Note that the value of ρ is constant for all model groups, and relative emigration rates increase (in areas of low fitness) or decrease (in areas of high fitness) with decreasing values of ρ and increasing values of $Z_{0,i}$ (Fig. 1). Changes in instantaneous M_i are the product of ρZ_0, thus changes in M_i for animals with higher natural mortality rates are more sensitive to changes in relative fitness. This parametrization of the movement model incorporates alternative life-history strategies among different model groups and uses the simple Ecopath input parameters (specifically $P/B = Z_0$) to define relative differences in response to fitness gradients. For example, blue sharks are a long-lived species (i.e., low risk to predation) and the need to respond quickly to changes in fitness gradients is less than that of mahi mahi (*Coryphaena hippurus*, a short-lived species with relatively high natural mortality). In a particular cell where fitness measures decrease for both species, movement rates will in-

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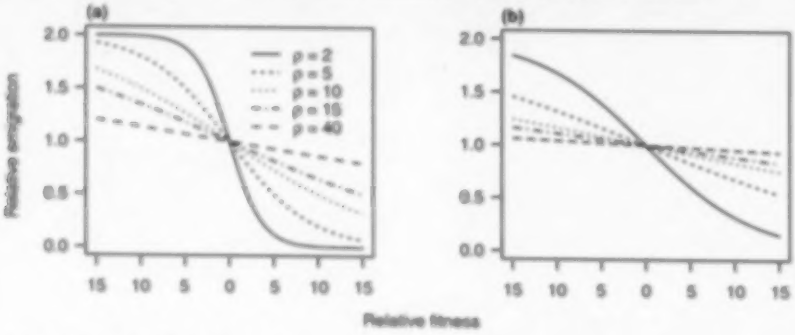
Fig. 1. Relative changes in emigration rates versus relative fitness for organisms with (*a*) $PIB = 0.5$ and (*b*) $PIB = 0.15$. As the value of ρ decreases, the relative change in emigration becomes more sensitive to relative changes in fitness.



crease more for mahi mahi than for blue sharks because of differences in longevity.

In both the VE and DM movement models, emigration rates from extremely productive cells are smaller than emigration rates from cells at equilibrium. Conversely, highly unproductive cells (or areas of high predation risk relative to foraging opportunities) have higher emigration than equilibrium cells. In the VE model, random movement occurs in all directions equally, with the exception of the adjustments to bias movement toward suitable habitats mentioned previously. In the DM model, we assume that animals are somewhat capable to detect spatial gradients in fitness (i.e., have an ability to detect gradients in f_i between adjacent cells). In the DM case, movement is directed towards adjacent cells with higher relative fitness, rather than uniformly in all directions, as in the VE model. The DM model allows species to more efficiently capitalize on productive spatial characteristics. In particular, if a highly productive area is present, such as a reserve, a prey species will strategically favor moving farther inside the reserve rather than out. The fitness gradient is calculated by taking the ratio of relative emigration rates of adjacent cells as shown in eq. 5. Here, G_{pq} is the gradient between cell rc and cell pq for all r rows and c columns and for each adjacent neighbor excluding diagonals.

$$(5) \qquad G_{pq} = H_{rc}/H_{pq}$$

At each time step for each cell boundary, instantaneous movement rate from rc to pq is set to $M_r \times G_{pq}$; this results in higher than average movement rates toward cells pq from cells rc that have lower relative fitness. The primary difference between the VE and DM models is that DM model assumes individuals can detect the direction in increased fitness opportunities and move towards areas of higher fitness. The VE model, however, assumes that individuals can only detect that fitness is greater elsewhere and move in random directions.

Habitat

The model area is defined by 0°N to 35°N and 150°W to 160°E and is represented as a grid consisting of 34 rows and 50 columns, where each grid cell is roughly 100 km in length or 10 000 km^2 in area. This represents a slightly smaller area than defined in the original model of Cox et al. (2002*a*); however, model units are specified on a per unit area basis. The cells were divided into two habitat categories, warm tropical waters and cool subtropical waters representing the northern transition zone (Fig. 2*a*). Each model trophic group was assigned preferred habitat type(s) (see Table 1) based on information from historical catch records. Groups for which there was no spatial information on its distribution were assumed to use both habitat types.

Physical features such as temperature, salinity, and oxygen concentrations that characterize habitats in the pelagic environment are all subject to dynamic change because of large-scale physical mixing processes (Lehodey et al. 1998). Convergence zones and fronts are important physical features that transport or advect plankton and microneckton (Yamamoto and Nishizawa 1986; Yoder et al. 1994). We represent this type of dynamic by incorporating a simple hydrodynamic model driven with surface current information, which is used to advect specified model groups and to create convergence zones and fronts.

Monthly surface current information was derived from ocean surface topography(as described in Boujean and Lagerloef 2002) and used as input data for calculating advection fields and upwelling velocities in Ecospace. Monthly mean surface current vectors were compiled from 15 November 1992 to 15 January 2003 for the model area defined above. At each monthly time step, surface current vectors were used to compute upwelling velocities for each spatial grid cell using R (R Development Core Team 2003). Upwelling brings cooler, nutrient-rich waters to the surface and enhances primary production. Downwelling results in convergence of water and concentration of organisms that can swim to prevent being downwelled. In the equatorial region, there is a relative decline in primary production from east to west. Currents along the equatorial region generally flow from east to west, and the depth of the thermocline increases farther west so that upwelling events simply turn over the relatively nutrient-depleted warmer surface layer. In the northern transition zone, currents generally flow from west to east (see Fig. 3).

Upwelling velocities were calculated assuming water mass balance (i.e., $dh/dt = 0$):

$$(6) \qquad \frac{dh}{dt} = V_v + V_u - D$$

where D represents the upwelling–downwelling velocity, and Vs are the net current flows (in the u and v directions) into each cell. This simple model (eq. 6) assumes depth is con-

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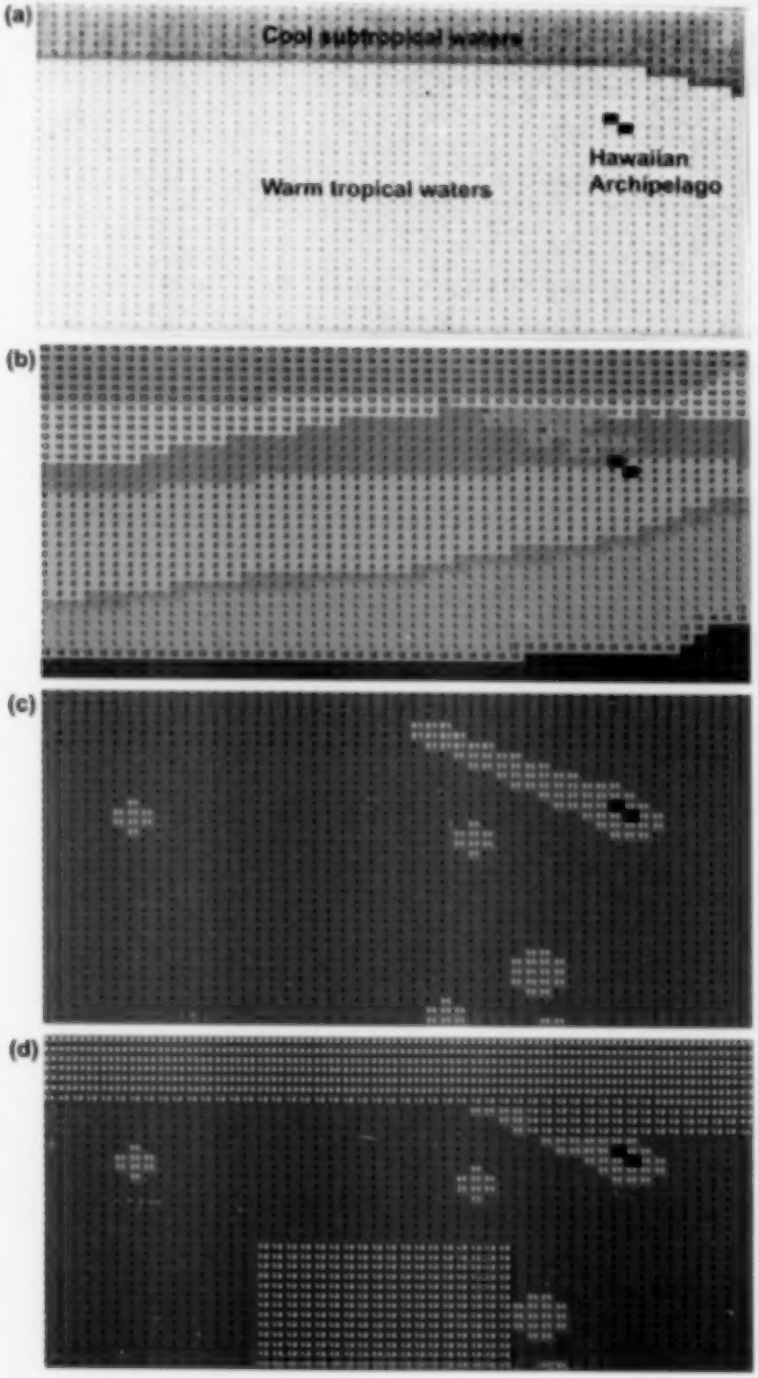
Fig. 2. (*a*) Habitat types defined in the spatial model, defined by relative differences in water temperature (small numbers). Cooler subtropical waters are shown in the north, and warmer tropical waters are in the south. The transition zone is approximated at 30°N. (*b*) Assumed spatial distribution of relative primary production, where warmer colors (i.e., red, orange) represent areas of higher primary productivity. (*c*) United States exclusive economic zones (US EEZ) (green), used as closed areas for foreign fleets in the status quo scenario, and closed to all gears in the US EEZ closure scenario. (*d*) Distribution of closed areas for the protected species scenario; note that domestic fleets were allowed to fish within the US EEZ that were not part of the larger closed areas.



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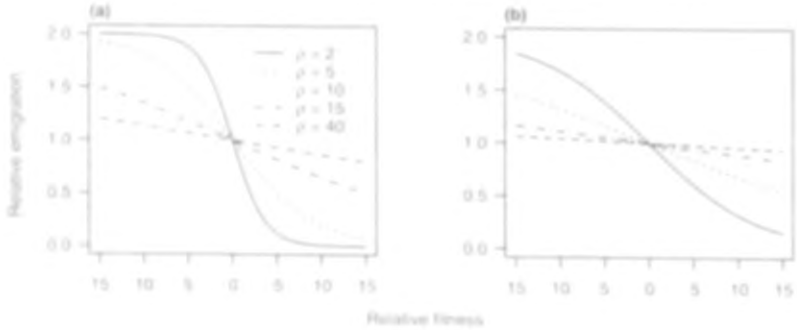

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$$(5) \qquad G_{xy} = H_n / H_{py}$$

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Upwelling velocities were calculated assuming water mass balance (i.e., $dh/dt = 0$):

$$(6) \qquad \frac{dh}{dt} = V_x - V_y - D$$

where D represents the upwelling/downwelling velocity, and Vs are the net current flows (in the x and y directions) into each cell. This simple model (eq. 6) assumes depth is con-

Fig. 2. (*a*) Habitat types defined in the spatial model, defined by relative differences in water temperature (small numbers). Cooler subtropical waters are shown to the north, and warmer tropical waters are to the south. The transition zone is approximated at 30° N. (*b*) Assumed spatial distribution of relative primary production, where warmer colors (i.e., red, orange) represent areas of higher primary productivity. (*c*) United States exclusive economic zones (US EEZ) (green), used as closed areas for foreign fleets in the status quo scenarios, and closed to all gears in the US EEZ closure scenario. (*d*) Distribution of closed areas for the protected species scenarios, note that domestic fleets were allowed to fish within the US EEZ that were not part of the larger closed areas.

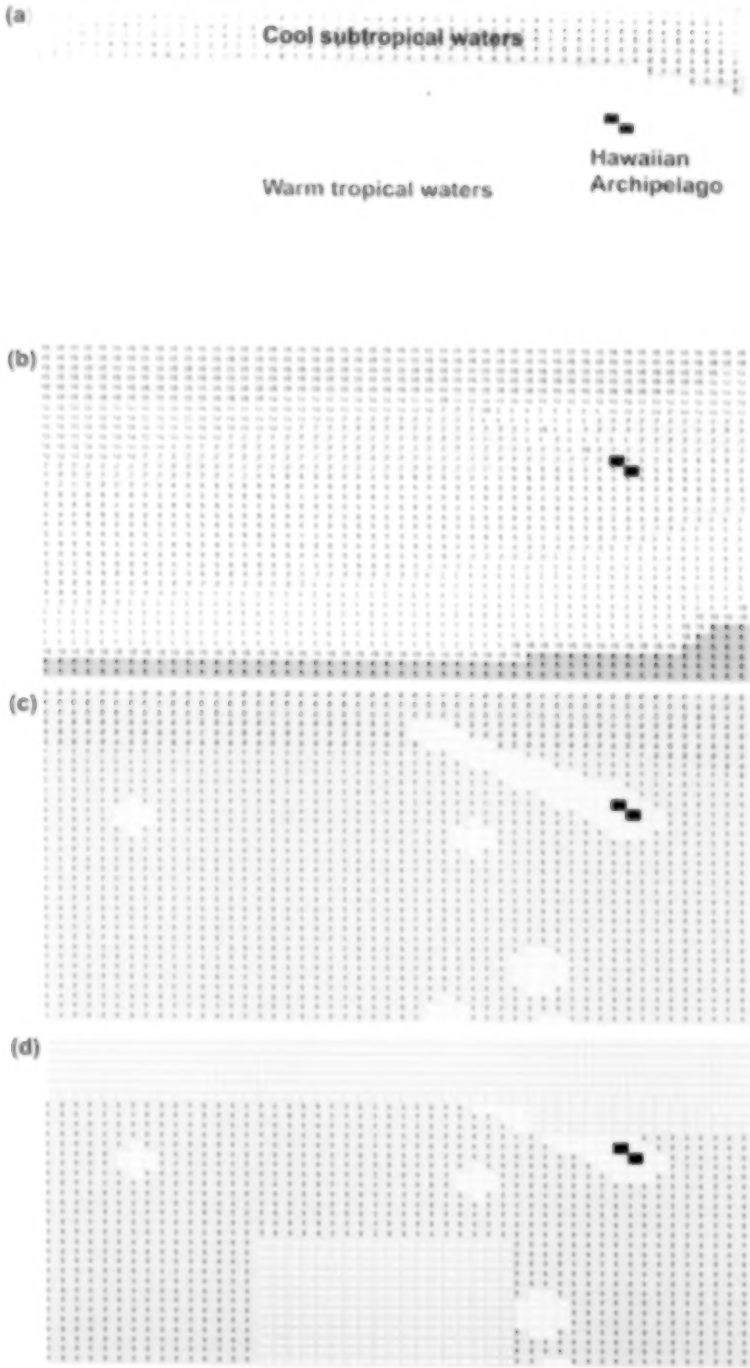

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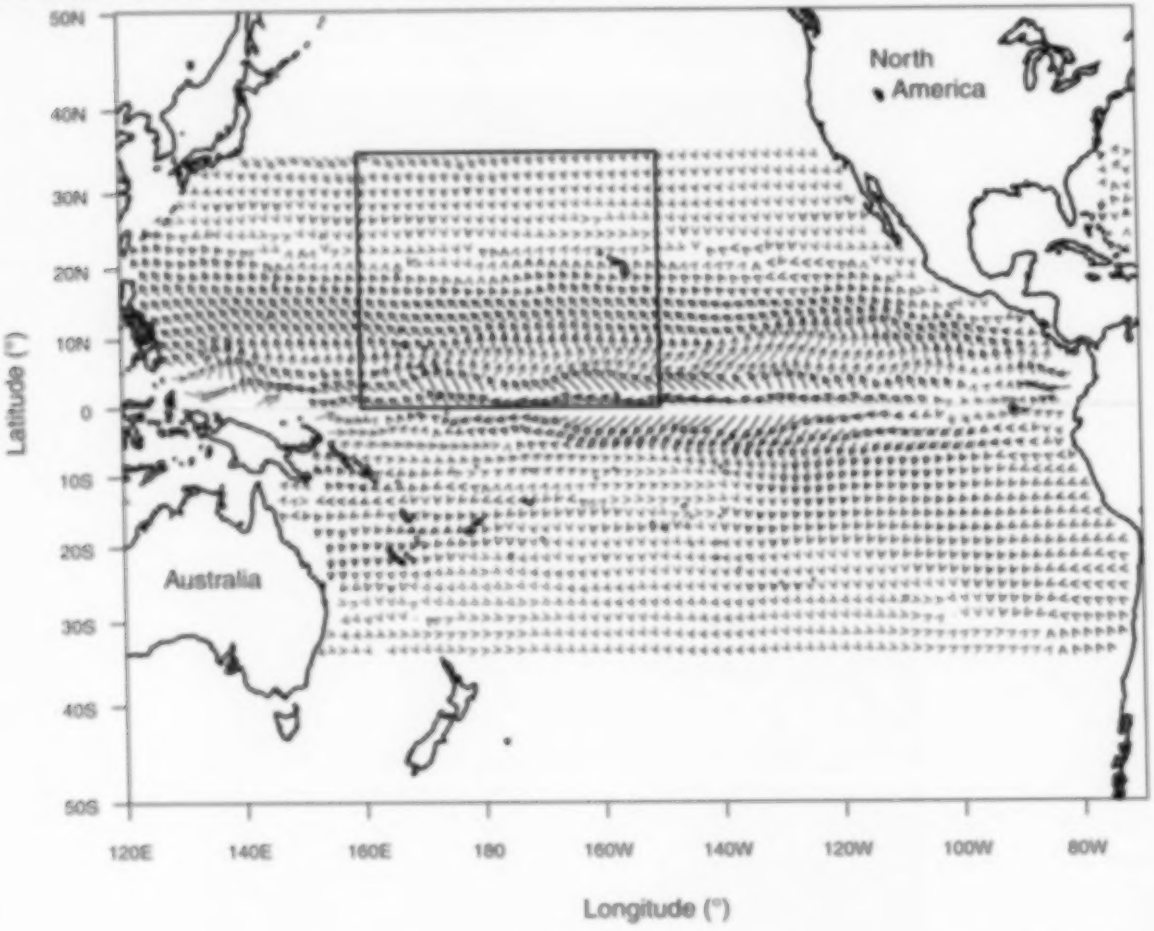
Fig. 3. Example of monthly surface current vector field (June 1992) used to calculate advection rates for zooplankton and spatial variation in primary production as a result of variable upwelling. Inset rectangle delineates the Hawaii box used in this model, and the red and blue arrows indicate eastern and western flowing currents, respectively.



stant over all grid cells. Primary production in each grid cell was assumed proportional to the rate of upwelling (i.e., $P_{rc} = \dot{q}P_{rc}/D$, where $\dot{q} = 0.5$ is a scaling parameter that approximates relative increases in primary production associated with increased upwelling, and P_{rc} is the total primary production in row r and column c) multiplied by relative rates of primary production (specified in Fig. 2*b*).

Spatial dynamics of fishing mortality

Total fishing effort for each fleet or gear at each time step was divided among all spatial cells that are open to fishing in proportion to an index of profitability for fishing in each cell. At each time step, a relative gravity weight ($G_{k,m}$) was calculated for each fishing fleet k spatial cell m:

$$G_{k,m} = \frac{O_{k,m}U_{k,m}\left(\sum_i p_{i,k}q_{i,k}B_{i,m}\right)}{R_{k,m}} \quad (7)$$

where $O_{k,m}$ and $U_{k,m}$ are cell-specific flags (0 or 1) specifying open or closed areas for each fleet (used to differentiate specific fishing grounds, or closed areas, for each fleet) and habitat associations for each fleet, respectively. In Ecosim, profitability is the price $p_{i,k}$ times catch $q_{i,k}B_{i,m}$ of all species per unit effort divided by the cost of fishing $R_{k,m}$ for gear k in cell m. Cost of fishing is generally broken down into two components: fixed costs (e.g., crew and gear) and variable costs (generally related to distance from port). Our interest in this application is in evaluating the efficacy of closed area policies in relation to alternative hypotheses about movement behaviors and dynamic habitat issues, so it was not necessary to correctly specify the relative cost of fishing over the entire grid area. We simply assumed the relative cost of fishing $R_{k,m} = 1$ in all cells and the gravity model simply responds to relative changes in biomass. Furthermore, we specified an increasing trend in fishing effort over 50-year period, therefore it was not necessary to specify the relative prices for various species that would normally be used in bio-economic models for predicting total fishing effort.

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Fishing mortality for each group, in each spatial cell, by each gear type, was then computed as

$$(8) \qquad F_{i,k,m} = \frac{F_{i,k} G_{k,m}}{\sum_{m} G_{k,m}}$$

where $F_{i,k}$ is the total fishing mortality rate imposed on species i by fleet k over all spatial cells. This spatial allocation of fishing effort closely approximates the ideal free distribution arguments; it tends to distribute effort among spatial cells such that profits are equivalent over all locations that are open to fishing (for more information on gravity models, see Caddy 1975; Hilborn and Walters 1987; and Walters and Bonfil 1999).

Simulation scenarios

We were interested in examining three specific issues concerning the use of closed areas as a management tool, assuming that effective fishing effort would continue to increase in the CNP. First, we wanted to compare the efficacy of MPAs assuming a near constant (or static) distribution of productivity and convergence areas in comparison to using current advection fields to predict the space–time distribution of primary production and convergence zones. Second, we wanted to compare alternative hypotheses about dispersal–movement dynamics in relation to MPAs. We examine each of these movement hypotheses in both the physically static model comparison as well as comparing alternative closed area policies. Finally, we wanted to contrast status quo fishing operations in the CNP with alternative closed area policies. Note that the locations of closed areas (shown in Figs. 2*c*, 2*d*) are not intended to evaluate any specific proposed policy in the CNP; they are simply alternative scenarios that were discussed among the authors as being likely scenarios and provided contrasting results for which alternative model assumptions could be addressed.

Longline and purse seine fishing effort has roughly doubled between 1952 and 1998 (Cox et al. 2002*b*); examples of technology improvements include the use of fish attraction devices in purse seine fisheries and night fishing with glow sticks in longline fisheries. For simplicity, we assume a doubling of effective fishing effort over the next 50 years in all simulation scenarios. All scenarios were initialized with the Ecopath base biomasses (the Ecopath model was constructed using biomass and mortality estimates from the 1990s), where initial biomasses for each pool or group were distributed equally over the assigned habitat types. In all scenarios, foreign fishing fleets were excluded from the United States exclusive economic zone (US EEZ), and the assumed value of the movement scale parameter was held constant for the fitness-driven dispersal models ($\rho = 10$).

First, we compared the effects of dynamic physical forcing with models with static physical forcing by comparing predicted changes in biomass (B_{50}/B_0) over a 50-year simulation period. We also make this comparison using all three movement hypotheses: advection–diffusion (AD) and the VE and DM models. This comparison was used to determine if dynamic physical forcing input data is important in predictions about of spatial policy options. In other words, is spatial variability in primary productivity and advection of zooplankton important in the design and implementation of closed areas? Preliminary simulations with no closed areas showed little difference in biomass ratios between dynamically and statically forced models when all areas were open to fishing. To create contrasting results between the physically forced model and unforced model, we closed a large area from 0°N to 35°N and 170°E to 180°E to all fleets year round, in addition to the US EEZ closures for foreign fleets. For the physical forcing scenarios, the 10-year current vector data (used for monthly advection and upwelling velocities) was recycled in sequence.

We then explored three alternative spatial policy options. Scenario 1, also referred to as the status quo option, excluded foreign longline and purse seine fleets from the US EEZ (see Fig. 2*c*). All United States fisheries were permitted to operate in all spatial grid cells, and no additional closures were implemented. In scenario 2, domestic fleets were also excluded from the US EEZ, and all fishing activity takes place in international waters only. From a United States perspective, this scenario may be the only enforceable closure. Scenario 3 was a protected species policy (Fig. 2*d*), intended to reduce bycatch of turtles and billfishes (e.g., blue marlin), and assumes that both domestic and international fisheries are excluded from closed areas.

Finally, we examined how sensitive policy options were to assumed values of ρ. Recall that ρ determines the sensitivity of animal movement to fitness gradients. Using the protected species scenario and the VE movement model, changes in biomass with $\rho = 5$, 10, 15, and 40 were compared. In addition, we made the same comparison with $\rho = 8$, 10, 14, and 40 using the DM model.

Results

For notation purposes, simulations that use monthly surface current information to calculate spatial and temporal changes in primary productivity are referred to as dynamic forced models, and simulations that use the long-term average primary productivities (Fig. 2*b*) are referred to as static forced models. During simulation runs using the static forced model, zooplankton biomass would accumulate in areas of higher primary production, resulting in a stationary distribution of zooplankton biomass. The distribution of zooplanktivores and their predators (e.g., small scombrids, squid, and other small pelagics) would roughly approximate the distribution of relative primary productivity and zooplankton. In contrast, during simulation runs using the dynamic forced model, zooplankton groups were advected by surface currents, resulting in an accumulation of biomass in convergence zones. Incorporating the monthly surface current vectors to advect zoolplanton groups provided a much more dynamic pattern that resulted in, more or less, seasonal distributions of phytoplankton (because of variability in upwelling) and zooplankton (because of surface current advection). The overall net effect of using the dynamic forced model resulted in spatial distributions of zooplankton biomass downstream of high primary production areas.

Biomass ratios, defined as the final biomass (B_{50}) divided by the initial biomass (B_0), were roughly 15% higher for simulations that included dynamic forcing than those for

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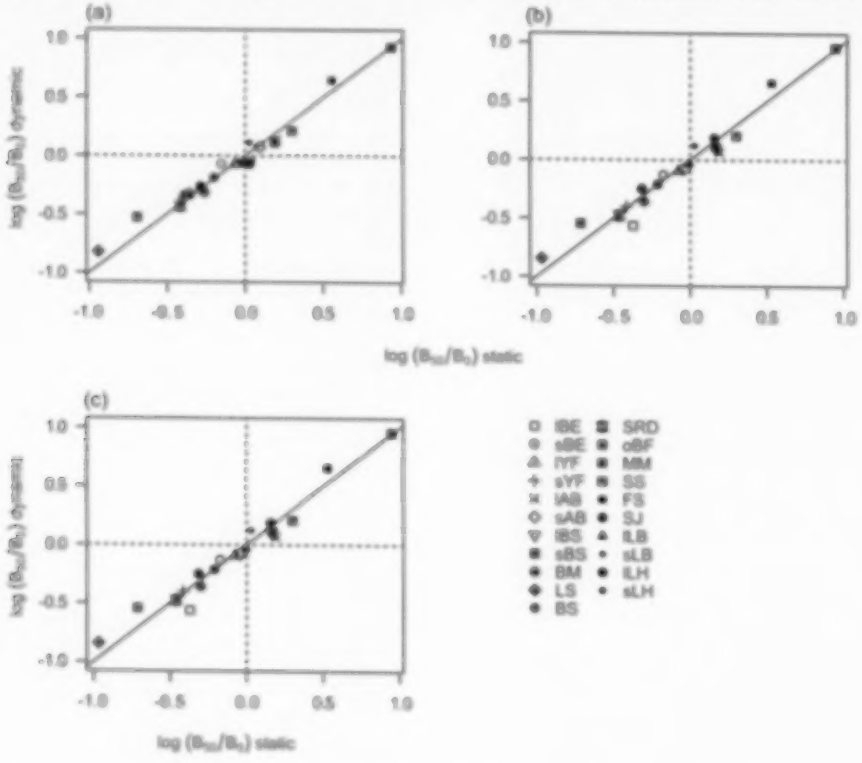
Fig. 4. Log biomass ratios (B_{50}/B_0) for models with (dynamic) and without (static) physical forcing, where panel (*a*) represents the advection–diffusion movement model, (*b*) the directed movement model, and (*c*) variable emigration movement model. The solid 1:1 line indicates no difference between B_{50}/B_0 ratios for dynamic forced and static forced models. Negative values imply a decline in biomass, and values below the 1:1 line indicate a larger decline in biomass for the dynamic forced model. See Table 1 for group codes.



simulations that used static forcing. This result, however, is due to the differences in calculated, total primary production between the two models (i.e., the scaling parameter $\hat{q}$ used to modify relative primary productivity in upwelling areas). Total annual primary production for simulations using the dynamic forcing was higher in comparison with simulations that simply used the long-term, average production or static forcing. The qualitative predictions in biomass changes between the physically forced and unforced models did not differ. However, to make fair comparison between the dynamic and static forced models, we subtracted the mean biomass ratio from each model, such that change in biomass ratio for all groups was standardized to a mean of 1.

There are small differences in B_{50}/B_0 ratios between dynamic and static forced models using the AD, VE, and DM models (Figs. 4*a*, 4*b*, and 4*c*, respectively). Each species or group has its own unique symbol, and values that fall on the 1:1 line indicate no difference in biomass change between the two representations of oceanographic spatial variability (dynamic vs. static forced models). Negative values represent declines in biomass over the 50-year simulation and vice versa. Where biomass declines are greater for the model with dynamic forcing, points fall below the 1:1 line. For example, the VE movement model predicted B_{50}/B_0 ratios for large bigeye tuna (lBE) equal to 0.69 and 0.57, for the static and dynamic forced models, respectively. For the AD movement model, changes in lBE biomass were nearly the same for dynamic and static models (i.e., point falls on the 1:1 line). Brown sharks (BS; *Carcharhinus* spp.), swordfish (SRD), and mahi mahi (MM) were least sensitive to assuming dynamic vs. static forcing for any of the movement models. Biomass was predicted to decline for large blue sharks (lBS) for AD movement model using static forcing, but to increase if they follow fitness driven dispersal rules (VE or DM movement models). Biomass declines were greater for blue marlin (BM) when dynamic physical forcing was assumed for all movement hypotheses, whereas other billfish (OBF) showed the opposite trend. In general, biomass differences for all groups were slightly larger when assuming the DM model. Regardless of which movement model was used, biomass ratios for all groups were slightly different between dynamic and static forced models. Based on these results (Fig. 4), we conclude that temporal variation in surface current vectors is important for the design and implementation of closed area policies. For all subsequent simulations, we incorporated the monthly surface current information for comparing alternative policies.

Despite a doubling of fishing effort over the 50-year simulation, in the status quo scenario biomass increased for small blue sharks (sBS), MM, neon flying squid (FS; *Ommastrephes bartramii*), and small scombrids (SS) for all three movement models (Fig. 5*a*). This increase in biomass

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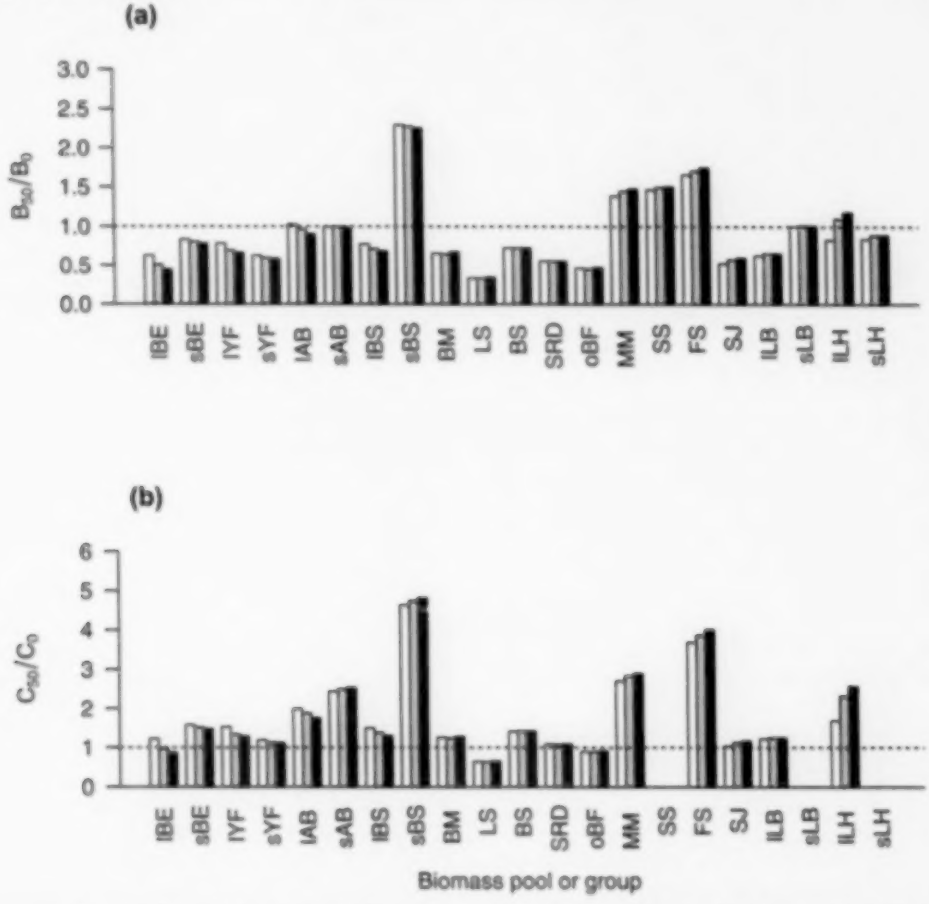
Fig. 5. (*a*) Biomass ratios (B_{50}/B_0) and (*b*) catch ratios (C_{50}/C_0) for selected pools or groups in the status quo scenario. The three bars for each group represent changes in biomass or catch ratios under the advection–diffusion movement (open bars), variable emigration (shaded), or directed movement (solid) models. Ratios less than 1 indicate a decline in biomass or catch over the 50-year simulation. See Table 1 for group codes.



was a consequence of reduced predation mortality by large predators, which continued to decline because of increasing fishing mortality. Large sharks (LS) are one of the primary predators on small blue sharks, and large shark abundance was severely reduced through bycatch associated with longline gear types. Large, commercially important species (lBE, small bigeye tuna (sBE), large yellowfin tuna (lYF), small yellowfin tuna (sYF), and SRD), as well as associated bycatch species (BM and LS), declined by up to 50% over the 50-year simulation (Fig. 5*a*).

Changes in biomass ratios were also sensitive to differences in movement hypotheses for most groups. The qualitative predictions about changes in biomass (either increasing or decreasing) were the same for all three movement models, with the exception of the large loggerhead turtles (lLH; *Caretta caretta*). In general, the magnitude of biomass changes from start to finish were greatest under the fitness driven dispersal hypotheses for groups with higher swimming speeds (Fig. 5), more so under the DM model. This result is a consequence of reduced fishing mortality within the US EEZs relative to areas that are open to both domestic and foreign fishing gears. Within the US EEZs, fitness measures were higher for large tunas and swordfish relative to fitness values outside the US EEZs because small prey items such as skipjack, mahi mahi (both fished species), and other small scombrids were at higher densities inside the US EEZs. In the status quo scenario (Scenario 1) under the fitness driven dispersal rules, total landings for domestic fleets increased, because of the increase in abundance within the US EEZs, and landings for foreign fleets decreased (Table 2).

A marginal increase in yields for the foreign longline fleet was predicted under the alternative policies (scenarios 2 and 3) over the status quo scenario (Table 2), and a marginal increase in yield for the domestic longline fleet was predicted under the protected species policy only. Yields for purse seine fisheries in the protected species policy were reduced because much of the juvenile tuna habitat was closed to fishing, and differences between foreign and domestic fleets were due to differences in initial catch compositions in the Ecopath model. Yields for longline gears were enhanced under the protected species policy because of reduced fishing mortality by purse seine fleets on juvenile tunas. Troll fish-

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Table 2. Predicted changes in total catch (C_{sq}/C_0) by fishing fleet for the status quo management scenario and all three movement hypotheses and predicted changes in catch ratios for the United States exclusive economic zone (US EEZ) closure and protected species policy.

	Status quo scenario (C_{sq}/C_0)			EEZ closures (% change)			Protected species (% change)		
Gear	AD	VE	DM	AD	VE	DM	AD	VE	DM
Domestic longline	1.39	1.40	1.42	94	93	93	101	104	105
Domestic purse	2.58	2.70	2.75	90	89	89	66	64	65
Pole and line	1.14	1.21	1.25	90	90	90	90	89	91
Troll	2.42	2.53	2.62	98	97	96	150	178	241
Foreign longline	1.44	1.29	1.22	101	103	104	101	109	115
Foreign purse	1.12	1.16	1.19	94	95	95	86	84	85
Other	1.31	1.33	1.35	96	97	98	76	76	76
Average	1.22	1.23	1.24	95	96	96	89	89	90

Note: Percentages greater than 100 indicate an increase in catch over the status quo scenario. AD, advection–diffusion movement model; VE, variable emigration movement model; DM, directed movement model.

eries for small albacore tuna (*Thunnus amalunga*) were enhanced under the protected species policy, especially for the DM model where a buildup of large sharks and other predators inside the MPAs resulted in increased dispersal rates for small albacore across MPA boundaries. In general, assuming the DM model resulted in higher yields for fisheries, increases in large predator abundances within MPAs makes these areas less fit for smaller tunas such as albacore and juvenile yellowfin. Overall, closing the US EEZ to all gears reduced the long-term catch by 4%–5% and adopting the protected species policy reduced long-term catch by 10%–11%.

Changes in biomass for the three different policy scenarios for each movement hypothesis were compared (Fig. 6). Closing the US EEZ to domestic fisheries resulted in only small differences in biomass ratios for most species relative to the status quo scenario, and the relative change is independent of which movement model was assumed. There was little to no difference in large bigeye tuna, large albacore, and swordfish biomass among scenarios, as the majority of these species are caught outside the US EEZ. Closing the US EEZ to all fleets (scenario 2) slightly reduced biomass of mahi mahi and small scombrids because large predators depleted these groups within the closed areas. Flying squid biomass increased slightly in scenario 2 for all movement hypotheses; this small increase was due to the slight reduction of small albacore, the primary predator of flying squid. Conversely, flying squid biomass declined in scenario 3 because of the large increase in small albacore biomass associated with the near complete closure of the fishing grounds in the north.

Changes in biomass ratios for the protected species policy (scenario 3) were markedly different for some groups in comparison with closing only a small proportion of the total fishing grounds (scenario 2). Under the AD movement hypothesis, small albacore tuna and skipjack benefitted greatly from large closed areas. Landings of small albacore were projected to increase under the protected species policy, despite closing much of the area where troll fisheries operate (Table 2). In this case, much of the troll fishing effort was predicted to occur near the edge of closed areas (28°N–30°N). Purse seine fleets (foreign), however, did not benefit from the protected species policy. Under the AD movement model, declines in biomass for large leatherback turtles (*Dermochelys coriacea*) and large loggerhead turtle were predicted to continue. However, under fitness-based dispersal rules, large loggerheads were predicted to increase 18% and 30% for VE and DM movement models, respectively. For blue marlin, changes in biomass were relatively the same for the AD model and VE model; however, marlin biomass was predicted to decline by an additional 10% under the DM model. In the blue marlin case, fitness measures were highest along the outside edges of closed areas because of a buildup of large sharks inside closed areas and increased abundance of juvenile yellowfin tuna outside the MPA boundaries. The net effect under the DM hypothesis was for blue marlin to actively migrate outside MPAs, which increased their capture probability.

Sensitivity to fitness gradients

Overall, the directions of predicted biomass change for both the VE and DM movement models were insensitive to assumed values of ρ (Fig. 7). Recall that smaller ρ values imply that emigration is more sensitive to relative changes in fitness, and this sensitivity is stronger for species with high *P*/*B* values (see Fig. 1). The large blue shark group was the most sensitive group to changes in ρ; as ρ increased in value (i.e., became less sensitive to fitness gradients), biomass ratios declined. In comparison with large bigeye tuna, large blue sharks have slower swimming speeds and a lower *P*/*B* ratio, and consequently spent more time exposed to fishing mortality because they were less likely to respond to the benefits of staying within the boundaries of an MPA when assumed values of ρ were high. Ironically, biomass declines for large tunas were slightly less when sensitivity to fitness gradients was reduced (i.e., $\rho = 15$ or $\rho = 40$). In this case, benefits to the adult pools were a result of reduced fishing mortality on juvenile pools, where juveniles were less sensitive to apparent predation risk inside MPAs for higher values of ρ.

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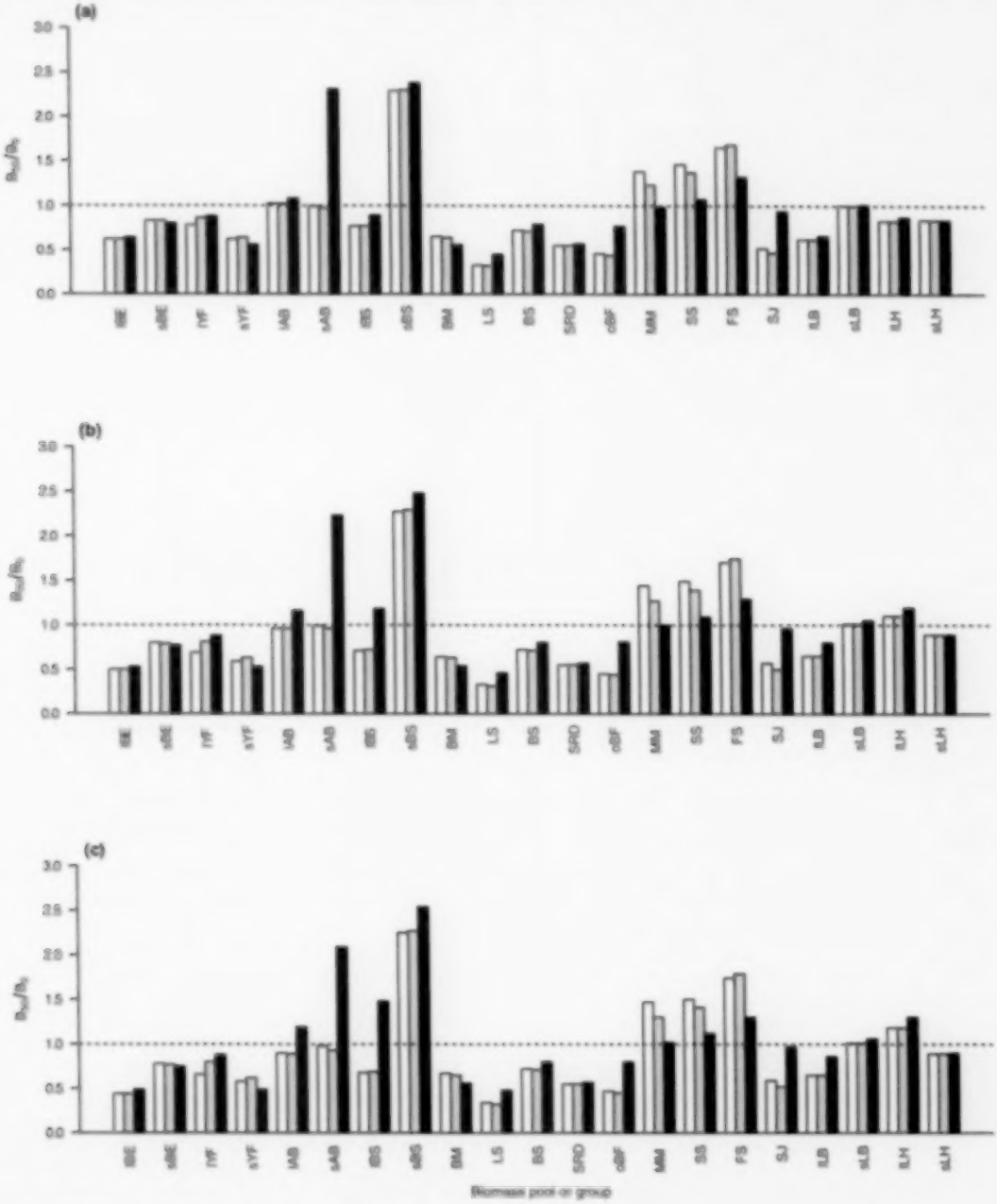
Fig. 6. Comparing changes in biomass for each group or pool for the status quo management scenario (scenario 1, open bars), United States exclusive economic zone (US EEZ) closures (scenario 2, shaded bars), and protected species policy (scenario 3, solid bars). Panel (*a*) shows results from the advection–diffusion movement model, panel (*b*) shows the variable emigration movement model, and panel (*c*) shows the directed movement model. See Table 1 for group codes.



Under the DM model, where it was assumed that fish could detect gradients and move to neighboring cells with higher fitness, changes in biomass relative to different ρ values were less in comparison with the VE model. Assuming directional movement into areas of higher fitness with strong responses to fitness gradients (i.e., DM model with low ρ values), the overall biomass distribution was similar in comparison with the AD model. The DM model, however, tended to concentrate fish (over a shorter time period) in areas of higher fitness where tuna groups were impacted more

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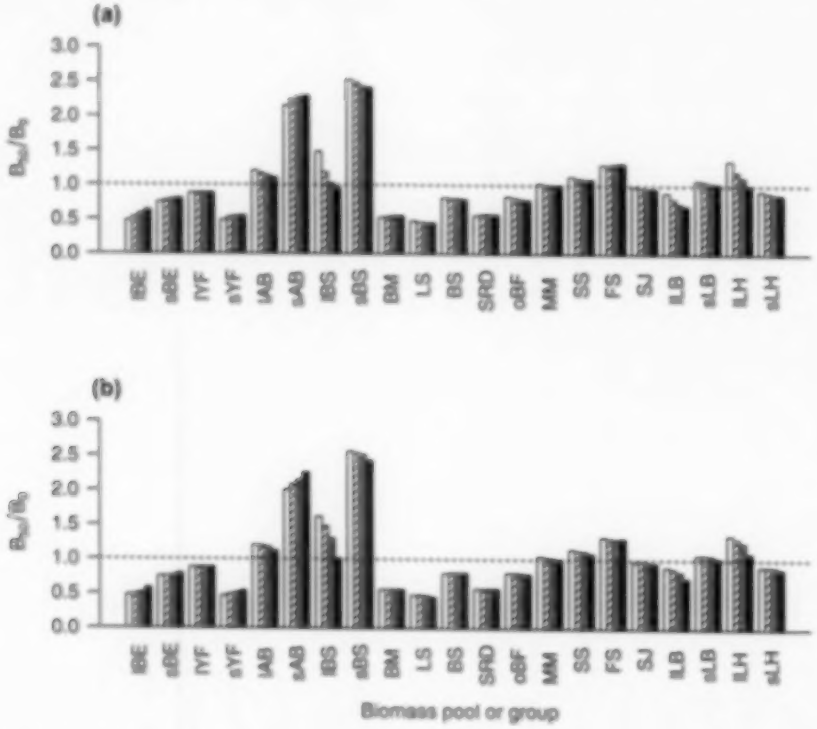
Fig. 7. Sensitivity of biomass changes for (*a*) the protected species policy assuming different values of ρ and variable emigration and (*b*) the directed movement model. Note that fitness gradients are steeper for smaller values of ρ. Values of ρ = (5, 10, 15, 40) in (*a*) and ρ = (8, 10, 14, 40) in (*b*) are represented by open bars, light hatching, heavy hatching, and solid bars, respectively. See Table 1 for group codes.



heavily by fisheries and other long-lived groups such as turtles, and blue sharks had higher biomass ration in comparison with the VE model.

Discussion

In this paper, we have compared three different closed area options, using three different assumptions about movement behavior, for fisheries in the central North Pacific Ocean. We were particularly interested in the consequences of closed area management policies where there is spatial variability in primary production and advection of zooplankton by surface currents. The analysis conducted by Lehodey et al. (1997) clearly demonstrated that the spatial distribution of skipjack tuna is largely influenced by zonal distribution of warm water, and the mean longitudinal position of warm water fronts varies by as much as 2000 km from year to year and by 4000 km within each year. Species distribution changes of this magnitude have large implications for spatial management policies, such as closed areas or MPAs, that are intended to reduce fishing mortality on target or nontarget species.

It was not surprising that we could draw few robust conclusions about the efficacy of MPAs for protection of pelagic fish communities. Changes in physical transport processes and assumptions about behavioral responses to changes in community structure led to divergent predictions about the efficacy of MPAs for some model groups. It is not likely that oceanographic monitoring and field data on fish distribution or behavior studies can resolve uncertainties about these assumptions in time to provide correct predictions about MPA responses prior to implementation of such policies. However, we were able to conclude that responses to alternative MPA policies were insensitive to assumptions about movements in relation to fitness gradients, and research efforts need not focus on this specific issue, at least in large, pelagic ecosystems. This implies that MPA policies should be treated as large-scale, adaptive management experiments and opportunities to learn about behavioral responses and monitored accordingly with clear expectation that they may fail in initial implementation.

It was not our goal to examine what the appropriate size or location of closed areas should be to optimize the tradeoffs between commercial fisheries and conservation. Interested readers on this topic are referred to Beattie et al. (2002) for an interesting application that considers both conservation and economics at the ecosystem level. The goal of the protected species policy (scenario 3) was an ad hoc attempt to reduce longline fishing mortality on sea turtles (loggerhead and leatherback turtles) and reduce fishing mortality on blue marlin. In comparison with the US EEZ closures (scenario 2), the protected species policy did reduce turtle bycatch; however, this reduction was insufficient to allow turtle populations to rebuild if fishing effort continues to

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double over the next 50 years. Much larger closed areas would be required to rebuild turtle populations or other gear modification that reduce the probability of capture for turtles. Surprisingly, blue marlin were predicted to decline even further under the protected species policy, especially when assuming the DM model. In this case, fitness measures for blue marlin were higher outside the MPAs because of large shark (a blue marlin predator) biomass accumulating in the closed areas and buildup of juvenile yellowfin tuna and small scombrids (marlin prey) along the boundaries of closed areas. For the simpler AD movement models, blue marlin continue to decline simply because the sizes of closed areas in the warm tropical region is insufficient, relative to the swimming speeds of blue marlin, to reduce fishing mortality associated with longline bycatch.

Ecospace is limited in its ability for MPA policy evaluation. It does not represent the details of species population dynamics, the full behavioral complexity of trophic interactions, or spatial organization of movement in terms of seasonal migration patterns. Furthermore, there is no quantitative way to compare predicted distributions of species biomass with historical spatial data, such as spatial catch per unit effort data, in Ecospace. Key parameters in the biomass dynamics (e.g., production/biomass ratios, food consumption rates, proportions of mortality accounted for by modeled interactions, diet compositions) cannot be estimated precisely for most species. There is also not enough comparative data on changes in ecosystem structure under large changes in fishing regimes to provide sound estimates of how much change would occur in predation rates (v_{ij}, v'_{ij} parameters). Despite these limitations, this modeling effort has provided some insights about the use of closed areas as a fisheries management policy option in pelagic ecosystems. Unlike reef-associated fishes, pelagic tunas and billfishes have much higher movement rates, and hence the size of closed areas must be larger for effective conservation in unregulated fisheries. Complex trophic interactions and behavior are not explicit in single-species MPA evaluations, where such interactions or behaviors may lead to cascades that result in further declines rather than the recovery of a species of conservation concern. For example, in our simulations presented here, predation mortality on small leatherback and loggerhead turtles increased because of increases in large sharks inside closed areas. Evaluating closed area policies from a single-species modeling perspective would not shed light on such potential negative effects.

There are two key points about including the physical oceanographic effects in Ecospace. (*i*) Because of surface current advection, the spatial distributions of phytoplankton and zooplankton do not strongly overlap, and the effects of increased primary production associated with upwelling are felt in convergence areas rather than the upwelling areas themselves. (*ii*) Interannual variability in surface current vectors can severely reduce the efficacy of MPAs because of spatial shifts in convergence zones. In the equatorial region, currents predominately flow from west to east and shear to the right in the Northern Hemisphere. Upwelling along the equator (in the eastern Pacific where the thermocline is shallow) brings nutrient-rich waters to the surface, resulting in increased primary production. At larger spatial scales (i.e., the entire Pacific Ocean), the spatial distribution of maximum zooplankton and tuna forage is further west relative to the intense primary production that occurs in the eastern equatorial Pacific (Lehodey et al. 1998). This spatial uncoupling of phytoplankton and zooplankton developed very clearly in the Ecospace model. At the smaller spatial scale, however, zooplankton and other forage species were distributed to the north because of currents shearing to the right into the tropical warm pools. Convergence zones, fronts, and eddy regions are important regions for tuna forage, as the zooplankton and forage species are advected to these regions (Laurs et al. 1984). In Ecospace, this advection created higher food concentrations for tunas and billfishes near the northern transition zone (roughly 30°N–35°N). Interannual variation in the strength and direction of surface currents plays an important role in the spatial distribution of tunas (Laurs et al. 1984; Lehodey et al. 1997). Changes in ocean circulation could reduce the efficacy of permanent closed areas because of spatial shifts in convergence zones and eddy regions. During extreme oceanographic anomalies, such as El Niño events, downstream production of tuna relative to areas of high primary productivity can shift dramatically. Areas that are typically high in tuna abundance, or areas where catch rates of nontarget species are high, can quickly become devoid of these species (Lehodey et al. 1998).

Figure 8 summarizes, in the form of biomass distributions along a transect through an MPA, simulation scenarios that involve closed area policies and models representing dynamic and static forcing and alternative movement behaviors. In this illustration, the equilibrium distribution of biomass for a top predator and their juveniles (where there is some cannibalism between the adult and juveniles) is represented in both unfished and fished situations. In the static forced model using AD movement rules, the distribution of forage and adult and juvenile predator biomass is roughly proportional to primary productivity in the unfished condition. Under fished conditions, the juvenile distribution remains roughly proportional to the distribution of forage; however, the density of targeted species increases within the MPA because of reduced total mortality. This contradicts the findings of Lehodey et al. (1998), where prey fields and predators were found downstream of high primary productivity areas because of current advection. Incorporating fitness-driven dispersal rules (VE or DM movement models) still does not capture the general pattern of nonoverlapping distributions or primary production and tuna distributions. Under this scenario, the distribution of forage and adult species is roughly the same as that under the AD movement model; however, the juvenile distributions are markedly different in response to increased predation risk. Juveniles actively avoid areas of high predation risk, and in cases where adult abundance has increased inside MPAs, the MPAs may afford no protection for juvenile groups. This is of particular concern where fisheries target juveniles or groups that are actively avoiding high predation risk areas (e.g., purse seine fisheries that harvest juvenile yellowfin tuna).

In an attempt to emulate the apparent downstream distribution of tunas and forage species relative to areas of high primary production, as well as the retention features of mesoscale eddies, we allowed zooplankton groups to be advected by monthly surface current information. This simple addition to the model complexity suddenly shifted the

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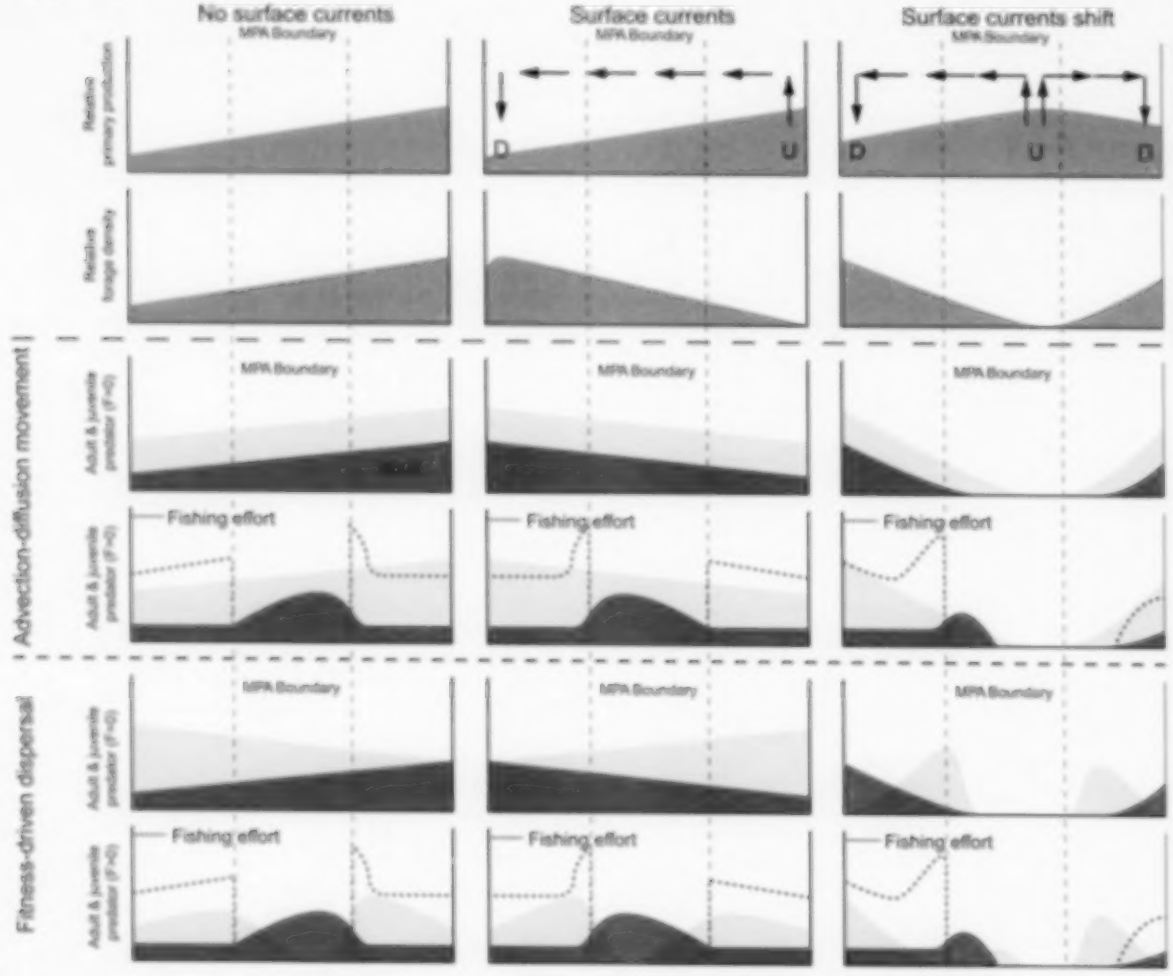
Fig. 8. A representation of the main Ecospace findings for closed area policies, with alternative movement models representing different hypotheses about animal behavior, and static forced distributions of production (first column) versus dynamic forced distributions of production, where monthly surface current information is used to predict spatial variability in primary production (second and third columns). The second row represents the spatial distribution of forage, where surface currents advect forage in the second and third columns. Each diagram represents a cross section or transect of the spatial distribution of abundance (and fishing effort) across an Ecospace map. Fishing effort distribution (predicted using eq. 7) for top predators is represented as the dotted line. Shaded polygons represent distributions of biomass along the transect at equilibrium; the area of each polygon is proportional to biomass. Vertical dashed lines represent marine protected area (MPA) boundaries; arrows represent current directions; U, upwelling; D, downwelling or convergence zones.



distribution of forage and tuna species downstream of high primary productivity areas. In upwelling regions, primary production was enhanced because of increased nutrient availability, and forage was concentrated downstream in convergence or downwelling regions. The overall distribution of adult and juvenile predators were now in agreement with the observations of Lehodey et al. (1998), but current advection had little affect on the outcome of spatial policy options. In effect, the use of the dynamic forcing appears to correctly represent the spatial distribution of each species relative to the distribution of primary production, but does not afford any additional protection from fishing in the form of closed areas. For example, Fig. 8 shows a simplified example where production of forage species is now inversely proportional to primary production, and the distribution of predators has simply reversed itself. The same total fraction of adult predators is vulnerable to fishing; the only real difference is that the tuna are now on the correct side of the ocean, per se. This is true regardless of which movement model is assumed.

Changes in ocean circulation can have profound effects on the efficacy of closed areas. In the case of the third column in Fig. 8, ocean currents shift such that the upwelling region now inside the MPA, and as a result adult predators tend to leave the MPA to areas where food is concentrated at or near convergence zones. Fishing effort is predicted to respond to

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the change in top predator distribution, where effort becomes less focused along the MPA boundary. The overall net effect of temporary changes in ocean circulation is a sudden emigration out of the MPA and an increase in total mortality owing to increased capture probability per unit of effort. There is also a corresponding shift in juvenile distribution because of changes in adult distribution, where predation risk is now higher outside the MPA.

Despite the apparent robustness of spatial policies to alternative hypotheses about mechanisms of dispersal, the spatial nonstationarity of oceanographic features that promote tuna production might lead to additional problems in the interpretation of fisheries data after the implementation of MPAs. If an MPA leads to accumulation of target species biomass only within the protected area, then catch statistics that are used to assess the status of fished stocks may not immediately reflect benefits of the MPA. Furthermore, a potentially dangerous situation may arise when oceanographic production processes shift and cause high densities of tuna to move outside protected areas, subjecting tuna to intense fishing pressure. In this case, catch rates would increase dramatically, and interpretation of nonspatial data using single-species stock assessment models would suggest the stock has suddenly increased in size. Management would then tend to maintain or even increase annual quotas. This misinterpretation of data would most likely lead to increases in fishing mortality that cause further depression in stock sizes.

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Behavior and recruitment success in fish larvae: variation with growth rate and the batch effect

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Abstract: Predation-mortality risk for red drum (*Sciaenops ocellatus*) larvae does not appear to be related to their growth rate, but important differences in behavioral performance occur between batches of larvae. This conclusion is based upon field-enclosure and laboratory experiments that assessed the degree to which predation-mortality rates and behavioral survival skills vary with growth rate. In field enclosures, populations composed of 15 fast-growing larvae and 15 slow-growing larvae of a comparable size were exposed to a predatory fish. Growth rate did not affect predation rate. In the laboratory we measured 11 survival skills on 100 larvae of a common size from 10 batches of eggs. For each batch, behavioral performance of fast-growing larvae was compared with that of slow-growing larvae. Growth rate did not affect performance in 10 of the 11 survival skills, but behavioral performance varied among treatment groups (growth rate × batch), with higher performance in most survival skills for some treatment groups and consistently poorer performance for other groups. This coordinated pattern of behavioral performance forecasts differential survival among batches. The variation among batches may be related to timing of spawning within the reproductive season of this serially spawning species.

Résumé : Le risque de mortalité dû à la prédation chez le tambour rouge (*Sciaenops ocellatus*) ne semble pas relié au taux de croissance, mais il existe d'importantes différences de performance comportementale chez les divers groupes de larves. Cette conclusion se base sur des expériences en laboratoire et en enclos en nature qui ont évalué à quel point les taux de la mortalité due à la prédation et les habiletés comportementales de survie varient en fonction du taux de croissance. Dans les enclos de terrain, nous avons exposé à la prédation par des poissons des populations de 15 larves à croissance rapide et 15 larves à croissance lente de même taille. Le taux de croissance n'affecte pas le taux de prédation. En laboratoire, nous avons évalué 11 habiletés de survie chez 100 larves de même taille provenant de 10 masses d'oeufs. Pour chaque masse d'oeufs, nous avons comparé la performance comportementale des larves à croissance rapide à celle des larves à croissance lente. Le taux de croissance n'affecte pas la performance de 10 de 11 habiletés de survie, mais la performance comportementale varie d'un traitement à l'autre (taux de croissance × masse d'oeufs); les meilleures performances dans la majorité des habiletés de survie se retrouvent dans certains groupes et les pires performances sont régulièrement dans d'autres groupes. Ce pattern coordonné de performances comportementales laisse présager une différence de survie chez les différents groupes. Les causes de la variation chez les différents groupes peuvent être reliées au moment de la ponte au cours de la période de reproduction chez cette espèce qui pond de façon répétée.

[Traduit par la Rédaction]

Introduction

Fluctuations in population sizes of many highly fecund marine organisms occur because of variability in the level of recruitment (Caley et al. 1996; Todd 1998). For fishes, recruitment variability is largely attributable to variable mortality of larval stages (Cushing 1975; Sissenwine 1984; Houde 1987). With the exception of catastrophic environmental events, factors affecting survival of larval and juvenile fishes are believed to be related by what Cushing (1975) called the "single process": as the length of time that larvae spend in a stage vulnerable to high mortality increases, the time over which the mortality operates also increases, thereby increasing cumulative mortality (Dahlberg 1979; McGurk 1986; Houde 1987). Moreover, it is clear that small changes in growth and mortality rates of larvae can generate order-of-magnitude or greater differences in annual recruitments (Shepherd and Cushing 1980; Davis et al.

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1991; Houde 2002), and that relationships among larval traits — size, growth rate, and behavioral processes such as foraging and predator defense — are critical for determining survival (Bailey and Houde 1989). Although causes of in situ mortality are rarely known explicitly (Sissenwine 1984; Houde 1987), it is clear that the factors that control predation rates ultimately can affect recruitment success.

A general paradigm has emerged from intuition that larger individuals are usually less vulnerable to predation and thus more likely to survive than smaller individuals (Anderson 1988; Miller et al. 1988; Rice et al. 1993*a*). This parsimonious and simple view places great emphasis on larval size as a factor in predation vulnerability and on growth rate as a controller of cumulative size-dependent predation mortality. Within virtually every cohort of fish there is appreciable variation in the growth rate of individuals. Evidence of this variability is commonly seen in the laboratory in the form of a size hierarchy or growth depensation, where the range of sizes of individuals increases with age (Blaxter 1988). For example, the coefficient of variation (standard deviation (SD) divided by the mean) for total length (TL) of red drum (*Sciaenops ocellatus*) larvae may increase from 5% to 15% during the second week posthatching (Smith and Fuiman 2003). Such variability has been attributed to elevated competition in dense cultures of larvae (Blaxter 1976), but the presence of two- to three-fold variation in growth rates within cohorts in large enclosures stocked at near-natural densities of larvae and zooplankton prey (Cowan and Houde 1990; Secor and Dean 1992; Folkvord et al. 1994), and considerable variation in size at age in field-collected fish (Fitzhugh et al. 1996; Rooker and Holt 1997) and larvae raised in isolation (Smith and Fuiman 2003), suggest that high variability in growth rate might be a natural phenomenon.

An obvious and important advantage of fast growth is the reduction in predation mortality by shortening the time that larvae spend in a stage vulnerable to high mortality (Cushing 1975; Houde 1987). Simulations using individual-based models have verified this contribution of growth rate to cumulative predation risk and the composition of the surviving population (e.g., Cowan et al. 1996; Letcher et al. 1996; Heath and Gallego 1997). However, experiments conducted in mesocosm enclosures indicate that under some circumstances, larger or faster growing larvae are more vulnerable to predators than smaller larvae (e.g., Fuiman 1989; Cowan and Houde 1992; Litvak and Leggett 1992). In addition, a recent field study showed an inverse relationship between growth rate and predation vulnerability that was independent of both size and time (Takasuka et al. 2003).

Thus, predation mortality is not determined solely by a size-based "window of vulnerability". The predation process ultimately decomposes into discrete events involving individuals and taking place over very short periods of time. The immediate outcome depends upon the behavior of predator and prey. In particular, the routine behavior of a larva will influence its likelihood of encountering a predator and, when it is challenged by a predator, evasive skills (including sensory and locomotor performance) are its ultimate hope for survival. Therefore, individuals will enjoy the lowest immediate predation risk if their behavior minimizes encounters with predators, their sensory capabilities allow them to perceive a threat and initiate a response, and their evasive performance maximizes the effectiveness of the response. The question arises, is predation mortality little more than the accumulation of deaths of individuals that were unfortunate enough to have encountered a predator during their vulnerable stage? Or is there a subset of individuals that have a suite of behavioral or physiological characteristics that confer greater fitness in predator–prey interactions, leaving less fit individuals to succumb to predators?

It has been suggested that the survivors of a larval year class are exceptional individuals (Crowder et al. 1992; Rice et al. 1993*b*; Heath and Gallego 1997), and field studies provide growing evidence of differential survival among individuals or cohorts of larvae (e.g., Rice et al. 1987; Meekan and Fortier 1996; Hare and Cowen 1997). Individuals and cohorts may benefit (or suffer) from spatial or temporal heterogeneity in extrinsic factors, such as food, predators, nursery habitat, and contaminants. But there may also be intrinsic variability in offspring viability that arises from variations in maternal investment in egg quality (e.g., Kjørsvik 1994; Chambers and Waiwood 1996). Such variations in investment may occur within a spawn or among spawns; the latter variation is referred to as a batch effect.

Here we investigate the possibility that exceptional individuals are those that combine fast growth with optimal antipredator behavior. Such a combination of attributes could be favored by natural selection, although recent studies of juvenile Atlantic silverside (*Menidia menidia*) showed that swimming performance was inversely related to growth rate, implying a trade-off between these traits (Billerbeck et al. 2001; Lankford et al. 2001). Nevertheless, there is also a mechanistic basis for a positive relationship. Growth rate and the sensory and locomotor capabilities that mediate all behaviors are fundamentally the products of physiological processes. The variation in growth rate observed within a cohort may be only the most obvious manifestation of more pervasive physiological variability among individuals. Such variability may affect all physiological processes, including survival skills that rely on sensory and locomotor performance.

We investigated the relationships between growth rate, behavioral survival skills, and predation mortality of red drum larvae in laboratory and field-enclosure experiments. Our objectives were to determine whether relative (within batches) or absolute differences in growth rate are associated with differences in behavioral performance and predation-mortality rate. We found no relationship between growth rate and either predation mortality or behavioral performance, but we did find significant differences in performance between batches of larvae (spawns). Closer examination of this batch effect suggested that behavioral performance might be related to variations in egg quality during the reproductive season of this serially spawning species.

Methods

The red drum has a reproductive strategy typical of many marine fishes. It is a generalized perciform fish that has high fecundity and spawns multiple times annually between mid-August and late November. It has planktonic eggs and estuary-dependent larvae that settle out of the water column

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at 4–6 mm TL to take up residence in seagrass beds (Rooker et al. 1998). We compared predation-mortality rates for fast- and slow-growing larvae in a field-enclosure experiment and compared the performance of behavioral survival skills by fast- and slow-growing larvae in a laboratory experiment. The larvae used in the laboratory experiment were those analyzed by Fuiman and Cowan (2003) but applied here to resolving different questions. Procedures for animal care and the laboratory experiment are summarized here; details were provided by Fuiman and Cowan (2003).

We obtained larvae with different growth rates without restricting diets or altering temperature, by taking advantage of growth-rate variability that is common in cultures of fish larvae (Smith and Fuiman 2003). In the laboratory, fast-growing larvae were selected for experiments when the first individuals in a tank reached the target length (7.5 mm TL; 63% of complete development based on the ontogenetic index (O_L) using complete squamation at 25 mm TL to define metamorphosis; Fuiman et al. 1998). Later, when the slowest growing individuals in the same tank reached the same target size, slow-growing larvae were removed for experiments. This provided a near-maximum range of growth rates and allowed comparisons of different batches of larvae, without artifacts from inducing growth-rate variability experimentally. In the mesocosm experiment, test populations were composed of larvae of similar sizes but different ages selected from cohorts of larvae being reared contemporaneously.

Animal care

Eggs were obtained from captive broodstock maintained at the Fisheries and Mariculture Laboratory of the University of Texas Marine Science Institute and the Coastal Conservation Association / Central Power and Light Marine Development Center hatchery (Corpus Christi, Texas) between July 1997 and May 1998 for the laboratory experiment and between June and July 1999 for the field-enclosure experiment. Broodstock were induced to spawn by manipulation of temperature and photoperiod; no hormonal injections were given. Each of four broodstock tanks contained 2 or 3 males and 2 or 3 females that spawned voluntarily. For each spawn (batch), 5000 eggs were incubated in a bucket. They hatched within 24 h of fertilization and were then placed in a 150-L conical rearing tank with aeration and a recirculating biological filter. Water temperature and salinity were maintained at 26.4 ± 0.7 °C (mean ± SD) and 30.1 ± 1.7 ppt, respectively. Larvae were maintained on a 12 h light : 12 h dark cycle with overhead fluorescent lighting providing illumination at 10 $\mu E \cdot m^{-2} \cdot s^{-1}$. Larvae were fed a mixture of rotifers (*Brachionus* sp.) and planktonic algae (*Isochrysis galbana* or *Nannochloropsis oculata*) once daily until 13 days posthatching. The larvae were fed newly hatched brine shrimp (*Artemia salina*) once per day from 10 days posthatching onward.

Field-enclosure experiment

Seven predation trials were conducted on 24 July and 4 August 1999 in cylindrical mesocosm enclosures, with three trials (enclosures) on the earlier date and four trials on the later date. Larvae were taken from three separate batches such that on each date fast growers from one batch were combined with slow growers of the same size from another batch. Each enclosure was 1 m in diameter by 3 m deep (volume 2.4 m^3) and suspended from a raft in waters adjacent to the University of Texas Marine Science Institute. Enclosure walls were constructed from 2-oz. blue Dacron sailcloth and the flat bottom panel was 53-µm nylon mesh (Nitex) with a 10 cm diameter hole at its center (plugged during deployment). Four external stainless-steel rings attached at 1-m intervals along the enclosures maintained each enclosure's shape during deployment. When deployed, approximately 0.5 m of each enclosure (not including the submerged 3 m) remained above the water surface to prevent loss of contents from enclosures or contamination from the surrounding water.

Prior to experimentation, otoliths of either fast- or slow-growing red drum larvae in one of the test populations were chemically labeled for subsequent identification. Larvae were removed from a rearing tank and placed in 4 L of alizarin complexone dihydrate (ALC) solution (50 $mg \cdot L^{-1}$) at a temperature of 27 °C. After 5 h of immersion, larvae were "rinsed" by siphoning as much of the ALC solution as possible and replacing it with clean, filtered seawater (~27 °C, 27 ppt). This rinsing process was repeated until the water had no visible traces of ALC. The larvae were then transferred to a 2-L mesh-sided (153 µm) holding chamber floating in their rearing tank. This procedure provided labeled larvae with the same water conditions as all other larvae, while separating them from the others prior to experimental trials. The group of larvae that was labeled alternated from trial to trial (i.e., slow growers in one trial, fast growers in the next), to eliminate any bias due to marking.

An assemblage of natural zooplankton (between 250 µm and 1 mm in size) was added to each enclosure at a concentration of approximately 90–100 zooplankters$\cdot L^{-1}$ (i.e., ~180 000 per enclosure). This zooplankton served as a food source for the larvae, as well as alternative prey for the predator. About 1 h after the alternative prey were added, 30 red drum larvae were introduced (15 fast growers from one batch and 15 slow growers from another batch) into each enclosure. Larvae were allowed to acclimate and disperse for ~12 h before a single predator (a pinfish, *Lagodon rhomboides*, 40–50 mm TL) was added to each enclosure. Pinfish are voracious predators of fish larvae and are common in the habitats occupied by red drum larvae (Fuiman 1994). In addition to the seven predation enclosures, eight enclosures were used as controls to establish the recovery rate for these trials. Control enclosures contained the same concentrations of larvae and zooplankton as the predation enclosures but without a predator.

Trials lasted approximately 6 h after introduction of the predators. After a trial, the contents of each enclosure were collected by removing the plug from the drain hole and lifting the enclosure from the water so that the water drained through the mesh bottom. As each enclosure was lifted, its sides were washed to free larvae that may have adhered. Predators were removed as soon as possible (within 5 min) to prevent additional predation on larvae as they became concentrated at the bottom during the recovery process. When each enclosure was removed from the water, its contents were placed in a 19-L bucket and returned to the laboratory, where the remaining larvae were removed, counted,

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and stored in 40% isopropyl alcohol until their otoliths could be examined for an ALC mark.

The numbers of fast- and slow-growing larvae recovered from an enclosure were used to compute instantaneous hourly mortality rates, after correcting for losses of larvae from control enclosures:

$$Z_r = -[[\ln(N_{t,r}^{P}/N_0) - \ln(N_{t,r}^{C}/N_0)]/t]$$

where Z_r is the corrected instantaneous hourly mortality rate for larvae of relative growth rate r (r = fast or slow), t is the duration of the trial in hours, N_0 is the number of larvae initially stocked, $N_{t,r}^{P}$ is the number of larvae of growth rate r recovered from an enclosure that contained a predator, and $N_{t,r}^{C}$ is the number of larvae recovered from a control enclosure (Fuiman and Gamble 1988).

Laboratory experiment

Three laboratory assays of behavioral performance were conducted on five fast-growing larvae and five slow-growing larvae from each of 10 replicate batches of larvae (100 larvae). The assays were routine swimming, acoustic startle stimulation, and visual startle stimulation, which yielded 11 variables (survival skills): routine swimming speed and, for each of the two types of startle stimuli, responsiveness, response latency, response distance, response duration, and response speed. Routine swimming speed is a measure of unstimulated movement and pertains to rates of encounter with predators and food items. The other performance variables are attributes of an evasive response that would be used when a predator attacks.

Each assay was repeated 5 times for each larva. Analyses of variability within individuals demonstrated that all variables were repeatable (Fuiman and Cowan 2003). Therefore, the data set for this study comprised the mean of each variable for each larva (n = 100 larvae). These means were based upon five trials for routine swimming speed, acoustic responsiveness, and visual responsiveness. The number of values contributing to the means for the remaining variables was the number of times (out of 5) a larva responded to the acoustic or visual stimulus.

Routine swimming was measured by placing a larva in a glass watch bowl with 1 L of seawater and recording its behavior for 2.5 min on videotape. The acoustic startle stimulus was a 500-Hz tone played at 5 dB above background through a loudspeaker (20 cm diameter) for a period of about 0.5 s. The visual startle stimulus was a black oval on a white card attached to a pendulum (after Batty 1989). When the pendulum was released from its resting position 17° from the bottom of its path, it accelerated toward an acrylic chamber containing a larva. A video camera recorded the larva's behavior in all assays.

Each set of experiments was conducted over a 2-day period. The routine swimming assay was conducted first, followed by the acoustic startle assay. Larvae were exposed to the acoustic stimulus once and then set aside in a sound-dampening box until the remaining four larvae were tested. This sequence was repeated until each larva was tested 5 times. Afterward, larvae were fed a small ration of brine shrimp and left undisturbed until the following day, when the visual startle assay was conducted. Each larva in turn was presented with the visual stimulus, until all larvae were tested 5 times. We examined the performance of individual larvae over the course of the five trials and found no evidence for habituation to either stimulus.

Analysis of video recordings included computer-assisted measurement of distances traveled by the larvae. Spatial resolution of these measurements was 0.4 mm per pixel for the routine swimming and acoustic startle assays and 0.2 mm per pixel for the visual startle assay. Durations of responses and latency of acoustic responses were measured by counting video fields (0.0167 s each). Latency of visual responses was determined from the electronic timer on the video display.

Statistical analysis

Growth rate of an individual was expressed in two ways: relative and absolute. Relative growth rate was a binary categorical variable (fast, slow) that identified whether an individual was selected as one of the fast-growing members of its batch or one of the slow-growing members. Absolute growth rate was a continuous variable that was independent of batch membership. It was calculated as a larva's TL (millimetres to the nearest 0.1 mm) minus length at hatching (2.77 ± 0.10 (mean ± SD; n = 40), divided by its age (days posthatching).

Field-enclosure experiment

The enclosure experiment directly examined the relationship between growth rate and predation mortality but without the behavioral information of the laboratory experiment. Results were analyzed as a single-factor (relative growth rate) paired-treatment experiment in which the mortality rate for fast-growing larvae in a particular enclosure was compared with the mortality rate of the slow-growing larvae in the same enclosure ($Z_f - Z_s$). This comparison was made with the nonparametric Wilcoxon's signed rank test and Student's t test for paired samples.

Laboratory experiment

Probability plots and skewness coefficients were examined to determine whether each of the 11 survival skills was normally distributed. Routine swimming speed, acoustic-response latency, and acoustic-response duration were strongly positively skewed, so a log-transformation was applied before statistical analysis. Acoustic and visual responsiveness were calculated as proportions of five trials in which each larva responded to each of the stimuli. Therefore, an angular (arcsine) transformation was applied to the square root of each value before statistical analysis to normalize the distributions, with corrections for a mean of 0% or 100% (Snedecor and Cochran 1967).

Effects of relative growth rate on the 11 performance measures were assessed by multivariate analysis of variance (ANOVA) and univariate ANOVA of the 100 larvae, using a mixed-effects model in a randomized-block design in which relative growth rate was a fixed effect and batch was a random blocking factor. This design allowed testing for differences in relative growth rate within batches and for differences among batches. Effects of absolute growth rate and batch on behavioral performance were assessed by analyses of covariance. The first stage of the analysis of covariance tested for a significant interaction term (difference in slopes among batches). When the interaction was not sig-

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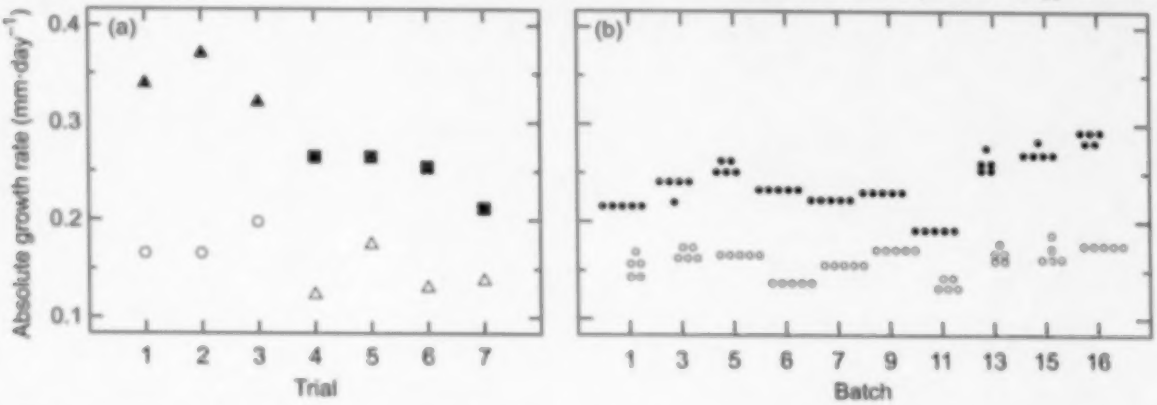
Fig. 1. Distribution of growth rates of populations of red drum (*Sciaenops ocellatus*) larvae used in field-enclosure experiments (*a*) and individual larvae used in laboratory experiments (*b*). The absolute growth rate is the difference between total length (TL) on the test date and length at hatching (2.77 mm TL) divided by age on the test date (days post hatching). Solid symbols denote larvae with fast relative growth rates; open symbols denote larvae with slow relative growth rates. The symbols in *a* identify batches. In *b*, batches are numbered consecutively; gaps in numbering are due to incomplete experiments, mass mortalities, or unhealthy batches of eggs or larvae.



nificant (equal slopes), the model was recomputed without the interaction term and the main effects (absolute growth rate, batch) were tested. The statistical power for tests of a growth-rate effect on predation-mortality rate and behavioral performance was computed to detect the null hypothesis that $\mu_1 = \mu_2$, using SAS® (version 8.2; SAS Institute Inc. 2001). All other statistical analyses were performed with SYSTAT® (version 10.2; Systat Software, Inc. 2002).

We explored patterns in behavioral performance among relative growth rates and batches of larvae with hierarchical cluster analysis. The data set for cluster analysis was summarized for each of the 11 performance variables by computing the means for each of the 20 treatment combinations of relative growth rate and batch. Each performance variable was standardized to a zero mean and unit variance to prevent the scale of any variable from biasing the analysis. Clusters were derived by applying hierarchical clustering to a similarity matrix of Euclidean distances for the 11 standardized variables. Three linkage methods were applied (complete, average, Ward) to examine the stability of the resulting clusters.

Results

Field-enclosure experiment

Fast-growing larvae came from two batches and were 16 or 19 days old with mean absolute growth rates of 0.34 and 0.25 mm·day^{-1}, respectively (Fig. 1*a*). Slow-growing larvae came from two batches (one in common with fast-growing larvae) and were 25 or 27 days old with mean absolute growth rates of 0.18 and 0.14 mm·day^{-1}, respectively. Larvae were 7.3 ± 0.76 mm TL (mean ± SD) overall, but despite efforts to use larvae of similar sizes, the mean length of fast-growing larvae was always slightly greater than that of slow-growing larvae in the same trial. Differences in mean TL between fast- and slow-growing larvae within a trial were 1.0 ± 0.70 mm (mean ± SD).

Larval recovery rates in the eight control enclosures ranged from 90% to 100% (mean recovery = 95%). At the end of a predation trial between 6 and 18 (mean = 11.1) of the 30 larvae were recovered from each enclosure. Taking control recovery data into account, instantaneous mortality rates for fast-growing larvae (Z_f) ranged from 0.06 to 0.33·h^{-1} and entirely included the range of mortality rates for slow-growing larvae (Z_s = 0.10–0.26·h^{-1}) (Fig. 2*a*). Mortality rates were greater for slow-growing larvae than for fast-growing larvae in five of the seven trials. Differences in mortality rate ($Z_f - Z_s$) within a trial averaged –0.04·h^{-1}, ranging from –0.19 to +0.12·h^{-1}. Disregarding the differences in TL, there was no difference in Z due to growth rate (Wilcoxon's test, $P = 0.23$; paired Student's t test, $P = 0.35$). To account for the potential effect on Z of the slight differences in size between fast- and slow-growing larvae, we computed residuals from a regression of Z against TL (Fig. 2*b*). Residuals for fast- and slow-growing larvae were not significantly different (Wilcoxon's test, $P = 0.50$; paired Student's t test, $P = 0.68$), from which we conclude that there was no difference in mortality rate due to growth rate even after we corrected for differences in size. The statistical power of the paired t tests, using the observed differences in Z between fast- and slow-growing larvae, was 0.14 (raw data) and 0.07 (TL residuals), owing to the very small differences between means and high variability within growth-rate groups.

Laboratory experiment

The 100 larvae tested were 7.7 ± 0.19 mm TL (mean ± SD), ranging from 7.1 to 8.2 mm TL. Mean absolute growth rates of larvae used in the laboratory experiment were similar to those of larvae used in the field-enclosure experiment (Fig. 1*b*). Growth of larvae within batches varied so much that the ages and absolute growth rates of fast- and slow-growing larvae did not overlap across the 10 batches. Fast growers ranged from 18 to 27 days old and had grown 0.19–0.29 mm·day^{-1}, whereas slow growers were 29–37 days old and had grown 0.13–0.19 mm·day^{-1}. Mean differences in age and growth rate within batches were 10.2 days and 0.08 mm·day^{-1}, respectively. One batch (No. 11) grew especially slowly, so the fast growers had a mean absolute

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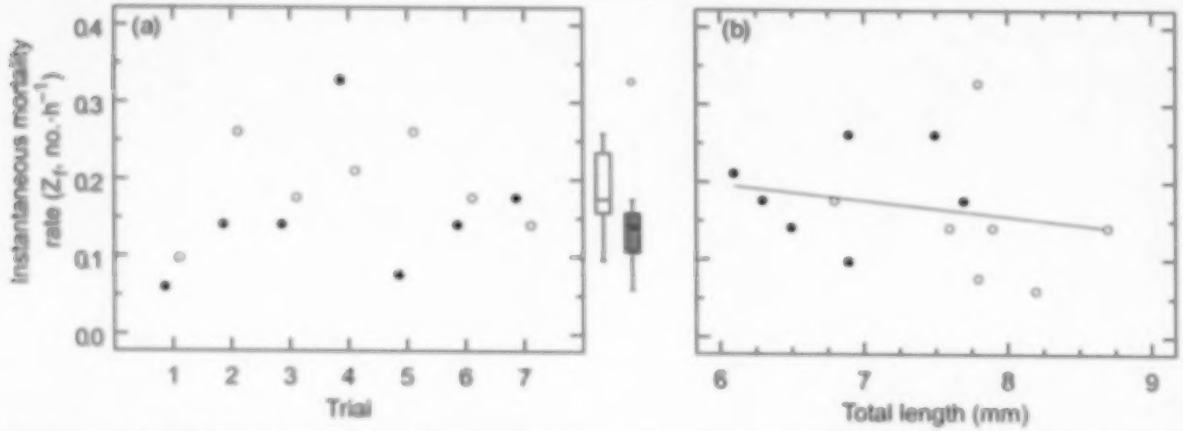
Fig. 2. (*a*) Instantaneous hourly predation-mortality rates for seven experimental groups of red drum larvae. Each group comprised 15 fast-growing larvae (●) and 15 slow-growing larvae (○). Experiments were conducted in field enclosures with a single predatory fish. Box diagrams on the right-hand margin of *a* summarize data for fast-growing (shaded rectangle) and slow-growing (open rectangle) larvae as the interquartile range (rectangle), median (horizontal line within the rectangle), range of values within 1.5 times the interquartile range from the median (vertical line), and unusually small or large values (circle). (*b*) Relationship between instantaneous hourly predation-mortality rates (Z) and mean TL of larvae for the same experimental groups. The regression equation (line) is $Z = 0.320 - 0.021$ TL ($P = 0.47$). Experiments were conducted in field enclosures with a single predatory fish.



growth rate only slightly greater than the slow growers of other batches (Fig. 1*b*).

Relative growth rate

Multivariate ANOVA indicated that relative growth rate had no significant effect on survival skills ($P = 0.159$). The statistical power of the multivariate ANOVA test for the observed effect of relative growth rate on all survival skills was 0.09. When survival skills were examined individually (univariate ANOVA), only visual-response duration demonstrated a significant effect of relative growth rate ($P = 0.015$; Fig. 3). Even though visual-response duration for fast growers (0.11 ± 0.02 s (mean ± SD)) was greater than for slow growers (0.09 ± 0.02 s), the difference within a batch was small (0.01 s ± 0.03; mean ± SD). Power calculations for individual survival skills (univariate ANOVA) were mixed, with some tests exhibiting acceptable power (0.89 and 0.96 for acoustic- and visual-response speed, respectively), moderate power (0.43) for acoustic responsiveness, and low power for the other variables (≤0.18). The statistical power was low because observed differences between fast- and slow-growing larvae were very small (generally <8% of the overall mean value of a variable). We consider this magnitude of difference in behavior, and in the predation-mortality rate (see the field-enclosure experiment), to be biologically insignificant, especially over the extremes of growth rate we observed.

In contrast to the lack of a growth-rate effect, there were significant differences in survival-skill performance among batches of larvae (multivariate ANOVA, $P < 0.0005$). Univariate F statistics showed that the growth-rate effect was significant ($P < 0.05$) for 6 of the 11 survival skills and marginal ($0.05 \leq P \leq 0.08$) for 3 others (Fig. 4). Only visual-response distance and visual-response duration were clearly not different between batches ($P = 0.248$ and $P = 0.511$, respectively). For many of the nine variables in which the batch effect was significant, one or two batches displayed extreme values relative to the other batches. For example, mean acoustic responsiveness was 57.4% overall, but batch 1 had a much higher mean (84.0%), whereas batches 15 and 16 had a much lower mean (30.0% and 32.0%, respectively; Fig. 4). Mean acoustic-response latency for batch 15 (0.05 s) was higher than the overall mean (0.03 s), owing to three larvae with very late responses. Acoustic-response distance averaged 9.2 mm overall, but batch 1 averaged 13.0 mm, which was 2.5 times the mean for individuals from batch 13 (5.3 mm). Overall responsiveness to the visual stimulus averaged 75.0%, but several batches had distinctly lower averages (34.0%, 54.0%, and 58.0% for batches 15, 16, and 13, respectively). Visual-response latency averaged 0.58 s overall, with a high mean value of 0.64 s for batch 16 and a relatively low value of 0.53 s for batch 9.

Absolute growth rate

Treating growth rate as a continuous random variable and analyzing effects with analyses of covariance produced only a few differences from the results for relative growth rate. The same single variable, visual-response duration, was significantly related to absolute growth rate ($P = 0.014$) but it lacked a batch effect ($P = 0.152$). However, simple linear regression of visual-response duration on absolute growth rate (batch effect omitted) showed that the relationship was not significant ($P = 0.097$, $R^2 = 0.029$).

Four of the 11 performance variables — routine swimming speed and acoustic-response distance, duration, and speed — displayed a significant interaction between absolute growth rate and batch, indicating that slopes of the relationships varied among batches. More specifically, most, but not all, batches showed no significant relationship between a survival skill and growth rate. Batches 1 and 13 displayed a significant negative relationship between routine swimming speed and absolute growth rate ($P \leq 0.021$, $R^2 \geq 0.508$). For batch 13, acoustic-response distance was negatively related to absolute growth rate, but the relationship was positive for

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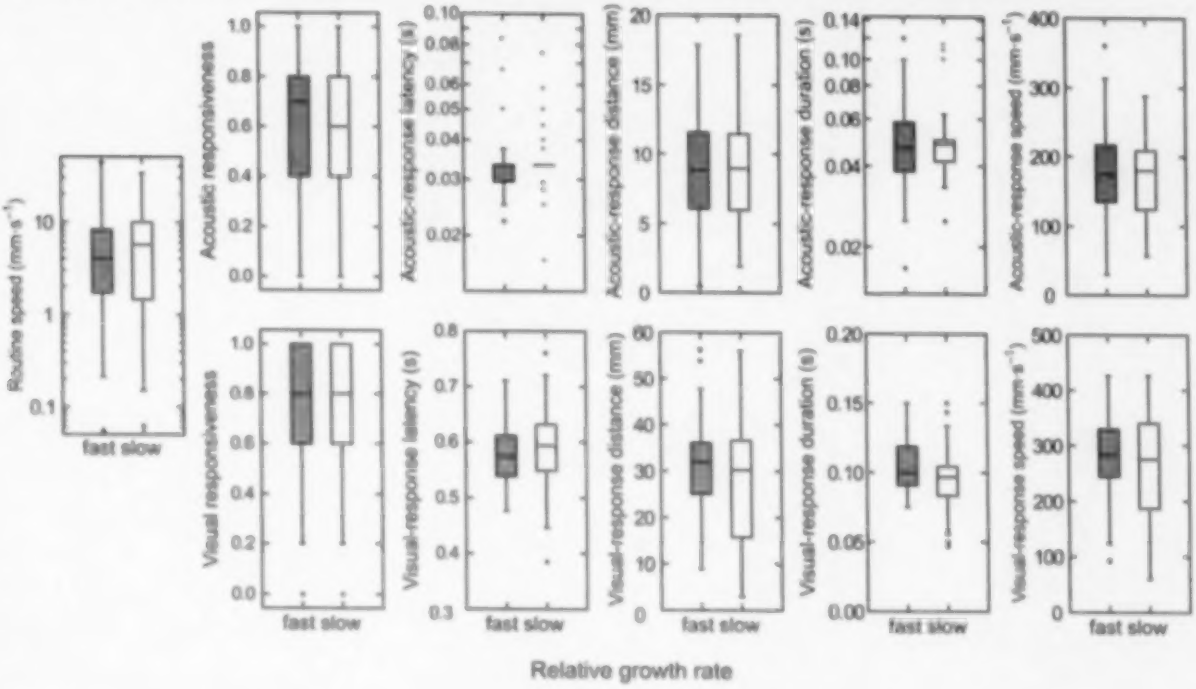
Fig. 3. Comparisons of behavioral performance of red drum larvae with fast and slow relative growth rates. Only visual-response duration varied with growth rate. Sample sizes are 50 larvae for routine speed and acoustic and visual responsiveness and 46–50 larvae for other variables, depending on responsiveness. Box diagrams summarize the data for fast-growing (shaded rectangle) and slow-growing (open rectangle) larvae as the interquartile range (rectangle), median (horizontal line within the rectangle), range of values within 1.5 times the interquartile range from the median (vertical line), and unusually small or large values (asterisk and circle).



batch 16 ($P \leq 0.038$, $R^2 \geq 0.436$). Acoustic-response duration was positively related to growth rate in batches 3 and 16 ($P \leq 0.045$, $R^2 \geq 0.512$). Both batches 9 and 16 showed a positive relationship between acoustic-response speed and growth rate, whereas batch 13 showed a negative relationship ($P \leq 0.044$, $R^2 \geq 0.416$).

Four variables that lacked a significant interaction term had a significant batch effect ($P \leq 0.011$), indicating that there were differences among batches in mean level of the behavioral performance variable. These variables were acoustic responsiveness, acoustic-response latency, visual responsiveness, and visual-response latency. Neither absolute growth rate nor the interaction term made a significant contribution to variation in these performance measures. Unlike the analyses of relative growth rate, the batch effects on the relationships between absolute growth rate and acoustic-response distance, duration, and speed were not significant. Differences in elevation for responsiveness and latency of acoustic and visual responses were attributable to a few batches. Batches 15 and 16 had relatively low acoustic responsiveness and batch 1 had high acoustic responsiveness. Batch 15 also had high acoustic latency. For visual responsiveness, four batches (11, 13, 15, 16) had low values compared with other batches. Batch 16 had relatively high visual-response latencies. Inasmuch as absolute growth rate did not have a significant effect on these performance variables, these differences mirrored those described for relative growth rate (Fig. 4).

Patterns in behavioral performance

The numerous significant differences in behavioral performance attributable to batches in both analyses, including significant interaction terms in the analysis of absolute growth rate, prompted a closer examination of the pattern of variability in behavior among the batches. Cluster analysis was performed on the 20 treatment groups (2 relative growth rates × 10 batches) rather than the 10 batches because of the significant interactions and because experiments were conducted on all members of a treatment group (but not all members of a batch) together. Two of the cluster linkage methods (complete, average) produced entirely concordant membership of two primary clusters (initial branching in Figs. 5*a* and 5*b*), although details of the relationships within each of these clusters differed. The third method (Ward linkage) assigned 15 of the 20 treatment groups to the same two clusters (Fig. 5*c*). The remaining five treatment groups, which formed a discrete subgroup in all three analyses, were placed in a different primary cluster by the Ward linkage method. Given the instability in the assignment of these five treatment groups, we regarded these intermediate treatment groups separately (cluster I in Fig. 5).

Inspection of mean values for survival skills of treatment groups revealed that the stable primary clusters (A, B) were quite distinct (Fig. 6). They were separated not on the basis of a few variables but rather according to differences in almost all survival skills. Means for each variable were always greater for cluster A than for cluster B. Formal comparison

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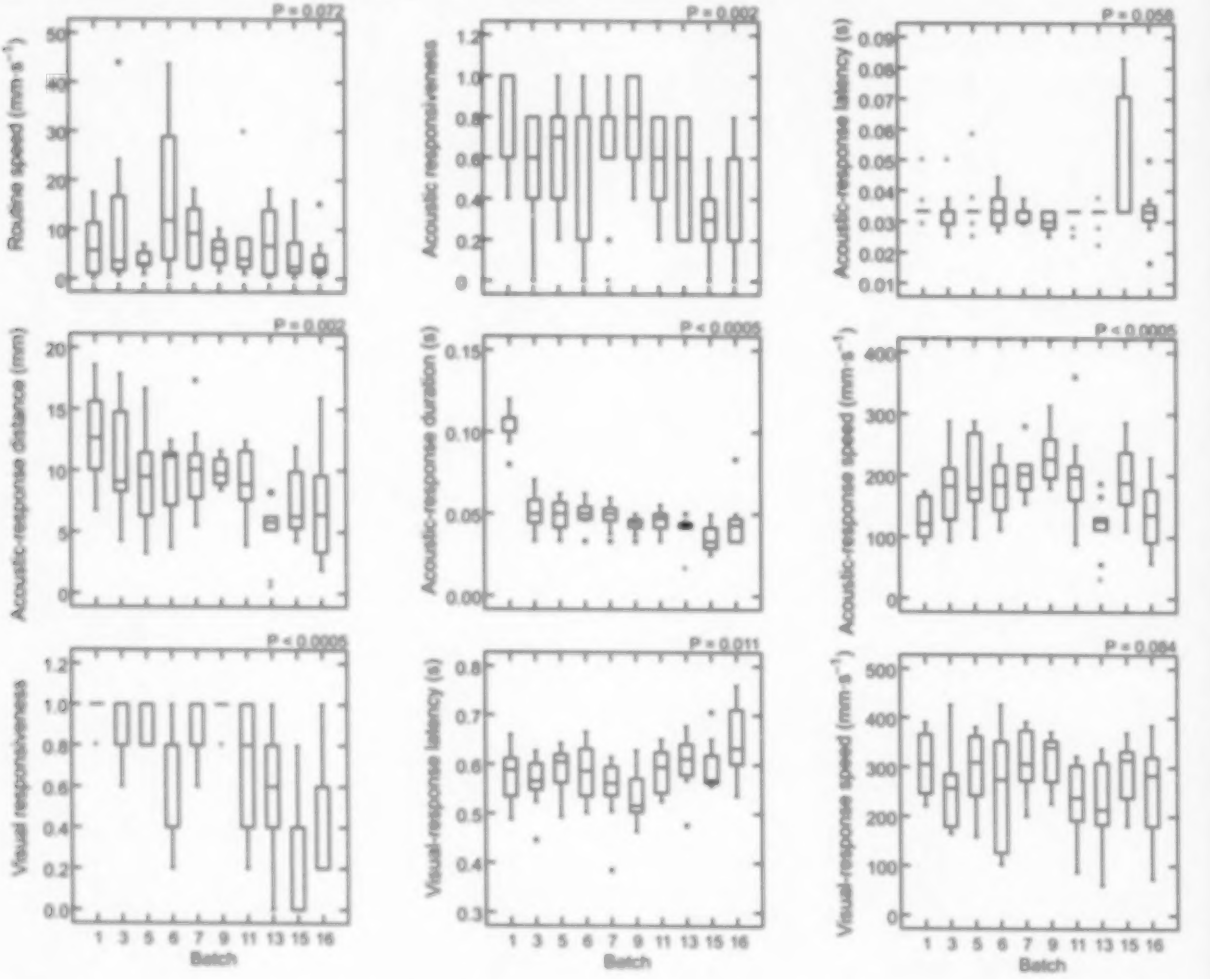
Fig. 4. Comparisons of behavioral performance of different batches of red drum larvae (growth rates are combined within each batch). Only survival skills for which there was a significant ($P < 0.05$) or marginally significant ($0.05 \leq P \leq 0.08$) batch effect are shown. Sample sizes are 10 larvae for routine speed and acoustic and visual responsiveness and 7–10 larvae for other variables, depending on responsiveness. Box diagrams summarize the data for fast-growing (shaded rectangle) and slow-growing (open rectangle) larvae as the interquartile range (rectangle), median (horizontal line within the rectangle), range of values within 1.5 times the interquartile range from the median (vertical line), and unusually small or large values (asterisk and circle).



of these clusters (two-sample Student's t test, $n = 9, 6$) revealed significant differences ($P \leq 0.044$) in 8 of the 11 variables. Only routine swimming speed, acoustic-response latency, and acoustic-response speed were not significantly different ($P \geq 0.113$). The most trenchant differences ($P \leq 0.008$) between clusters A and B were for visual responsiveness (averaging 89.8% and 53.0%, respectively), visual-response distance (32.6 and 22.9 mm), acoustic responsiveness (74.2% and 42.7%), acoustic-response distance (11.1 and 6.3 mm), and acoustic-response duration (0.057 and 0.037 s) (Fig. 6).

Subgroup I, which was variously assigned to cluster A or cluster B, displayed intermediate levels of behavioral performance. Mean values for visual responsiveness (73.5%) and acoustic-response distance (8.9 mm) and duration (0.047 s) were midway between the corresponding values for clusters A and B (Fig. 6). However, this intermediate subgroup was more similar to cluster A in terms of visual-response distance, duration, and speed, but more similar to cluster B in terms of acoustic responsiveness and visual-response latency.

Discussion

A direct link between larval growth rate and predation vulnerability has been the subject of some debate (Bailey and Houde 1989; Leggett and Deblois 1994; Takasuka et al. 2003). Our experiments demonstrate that growth rate and predation vulnerability are not related, positively or negatively, in red drum larvae at this stage of development. This conclusion is based upon separate comparisons of predation-

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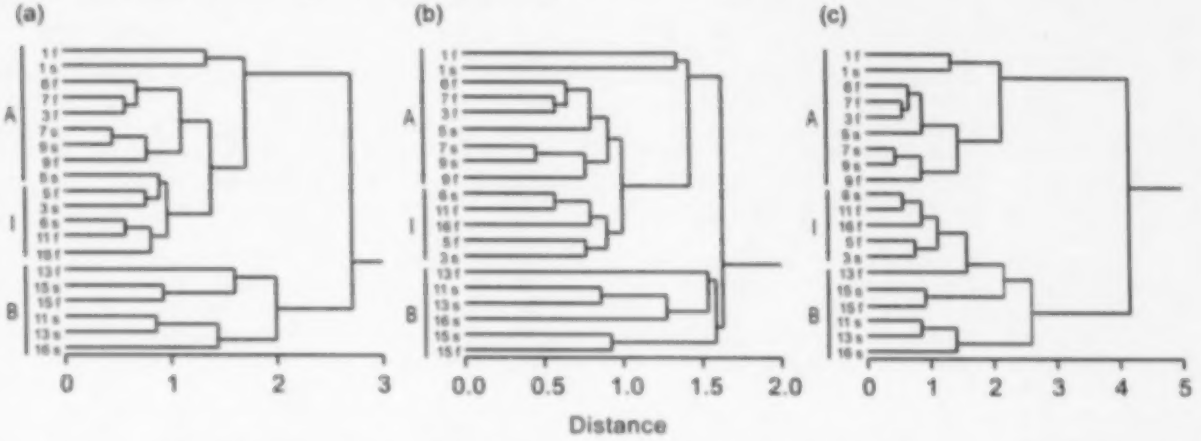
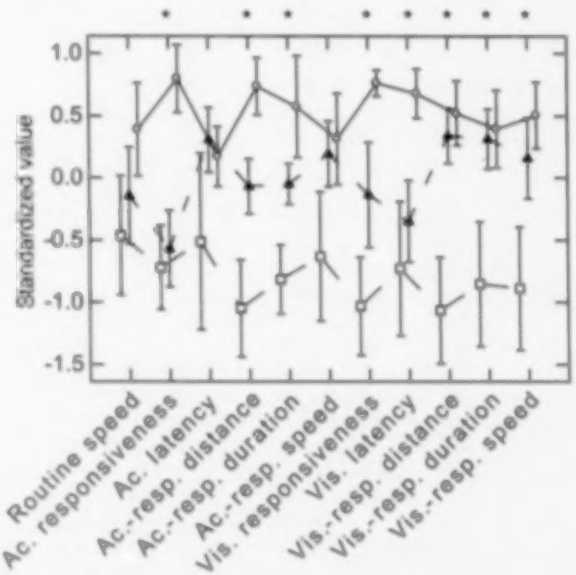
Fig. 5. Relationships among 20 treatment groups of red drum larvae (2 growth rates × 10 batches) based on the similarity of their behavioral performance (11 variables) derived from hierarchical cluster analysis (complete linkage (*a*), average linkage (*b*), and Ward linkage (*c*) methods). Cluster analyses identified two stable clusters (A, B) and one intermediate cluster (I). Codes at ends of branches identify batch number and relative growth rate (fast (f) or slow (s)).



mortality rates and behavioral mechanics of predator evasion. Our conclusion is supported by the study by Bertram and Leggett (1994), who conducted experiments in 7-L laboratory containers to compare predation mortality of winter flounder (*Pseudopleuronectes americanus*) larvae that varied in age at metamorphosis but not in length at metamorphosis. Using a shrimp (*Crangon septemspinosa*) as the predator, they too were unable to establish any difference in instantaneous predation mortality for larvae of different ages (i.e., mean growth rate histories). We concur with Bertram and Leggett (1994) that any differences in instantaneous predation vulnerability between same-sized larvae of different growth-rate histories are "subtle and potentially ecologically inconsequential", provided the slower growing larvae are not malnourished. But this differs from the field observations of Takasuka et al. (2003) and their proposed "growth-selective predation" hypothesis.

In previous research studies in which a relationship between larval growth rate and predation vulnerability was discussed, larval size (independent of larval nutritional condition) was often a confounding factor. For example, in studies suggesting that predation vulnerability decreases with larval growth rate (Miller et al. 1988; Bailey and Houde 1989), larval size, rather than growth rate, probably had the greater effect on mortality. Many studies have shown that larger individual larvae tend to be less vulnerable to predation (Anderson 1988; Miller et al. 1988; Fuiman 1994) because of a decrease in the number of potential predators and an increase in escape ability as larvae become larger. Yet in-situ enclosure experiments (Fuiman 1989; Litvak and Leggett 1992; Cowan and Houde 1992) and modeling simulations (Cowan et al. 1996; Letcher et al. 1996; Paradis et al. 1996) have indicated that under some circumstances, larger larvae are more vulnerable to predators than smaller larvae. This result is believed to be due, in part, to increased encounter rates attributable to higher swimming speeds of larger larvae, and increased larval pigmentation and movement that may make larvae more conspicuous to predators

Fig. 6. Mean performance for clusters identified in Fig. 5. Lines connect standardized (mean = 0, standard deviation = 1) mean values for each performance variable of cluster A (○, $n = 45$ larvae), cluster B (□, $n = 30$ larvae), and cluster I (▲, $n = 25$ larvae). Vertical lines through means represent ±1 standard error. An asterisk indicates a significant difference ($P < 0.05$) between cluster A and cluster B. The sign for the standardized value of acoustic- and visual-response latencies was reversed for better comparison with other variables. Ac., acoustic; vis., visual; resp., response.



(Bailey and Houde 1989; Fuiman and Magurran 1994). Larger larvae also may be at a disadvantage when encountering predators that preferentially attack larger prey (Litvak and Leggett 1992), or nonvisual predators, such as jellyfish,

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because of increased prey target size (Bailey and Batty 1984; Litvak and Leggett 1992). Simple and parsimonious conceptual models that relate larval size to predation vulnerability as a monotonic function are therefore difficult to defend (Cowan et al. 1997). The importance of size to the staging and outcome of a predator–prey interaction (immediate mortality) does not, however, diminish the importance of larval growth rate as a regulator of cumulative cohort-specific mortality rate. Growth rate determines the span of time during which predation-mortality risk is especially high and, in this way, determines cumulative mortality, as has been well demonstrated by both conceptual arguments (Cushing 1975; Houde 1989) and modeling studies (Cowan et al. 1996, 1997; O'Neal 2002).

Our finding of no difference in predation-mortality rates between fast- and slow-growing larvae in field enclosures must be considered in light of the fact that survival-skill performance in the laboratory experiment varied among batches of larvae. It was not possible to determine whether there was a batch effect in the enclosure experiment because fast and slow growers of the same size could not be placed in the same enclosure on the same day.

The batch effect on behavioral performance was pervasive, in contrast to the absence of a growth-rate effect. We did not expect such strong differences between the replicates (batches) and so this batch effect merits closer scrutiny in future experiments. The batch effect was present directly (main effect) or indirectly (interaction) for 8 of 11 survival skills. A pattern of variation in the broad array of survival skills emerged, in which treatment groups (relative growth rate × batch, the individual elements of the interaction term) were characterized by a common level of performance for most survival skills, rather than proficiency in one or a small set of skills. The 20 treatment groups fell into three classes, two of which represented distinctive extremes of behavioral performance (clusters A and B in this study).

Differences between clusters A and B were many and the magnitudes of these differences were ecologically meaningful. The difference in responsiveness to the visual stimulus paralleled the difference in responsiveness to the acoustic stimulus, a pattern we previously observed at the level of individual larvae (Fuiman and Cowan 2003). Initiating a response to a threatening stimulus is the first and most critical stage in predator evasion because only after a response begins do aspects of its timing, magnitude, and direction come into play. If our measures are relevant to the natural predation scenario, the difference of 32–37 percentage points in responsiveness could translate into a substantial difference in mortality between batches. For example, laboratory experiments showed that pinfish (14–15 cm TL) caught 98% of non-responding red drum larvae of the size studied here, whereas they caught 57% of responding larvae (Fuiman 1994). These percentages, when applied to mean visual- and acoustic-responsiveness values observed in the current study, predict that larvae from treatment groups in cluster A would survive 32%–39% of attacks, but that larvae from treatment groups in cluster B would survive 19%–24% of attacks.

These calculations, however, do not take into account the coordinated differences in other survival skills that coincide with differences in responsiveness to further enhance the survival of cluster A larvae relative to cluster B larvae. Cluster A larvae traveled 5–10 mm farther during a response, and approximately 40–60 mm·s^{-1} faster, although their responses lasted only 0.02 s longer (i.e., faster acceleration). The optimal strategy for predator evasion by a fish larva attacked by a larger fish is rapid acceleration that takes the larva out of the predator's path in the final moments of the attack (Blaxter and Fuiman 1990; Fuiman and Magurran 1994). Cluster A larvae also had a 0.05 s shorter latency in their response to the visual stimulus. This earlier response corresponded to a mean reactive distance of 21.9 cm from the accelerating stimulus, compared with 16.5 cm for cluster B larvae. This left larvae with an average of 0.22 and 0.17 s (clusters A and B, respectively) before the "predator" would have made contact had the larva not responded. Therefore, the opposite sign of the difference in response latency between clusters A and B is fully concordant with the other variables: a negative difference or earlier response signifies better performance (a greater distance between predator and larva and more time to escape). The benefit of ever earlier responses does not increase indefinitely, however. Very early responses are detrimental because they allow the predator sufficient time to correct its attack path to intercept the moving prey (Fuiman 1993; Fuiman and Magurran 1994). Overall, the earlier response and seemingly small advantage in response distance for cluster A larvae amplify the effect of their heightened responsiveness on the probability of surviving a predatory attack.

An obvious and important question, given the presence of a batch effect on larval performance and its likely importance to predation-mortality risk, is, What is the cause of the batch effect? Our experimental design did not allow us to draw definitive conclusions, but we can comment on the most obvious possibilities: variations in rearing conditions or in egg quality. It is unlikely that rearing conditions varied enough to generate differences in behavior. We maintained reasonably constant conditions of temperature, salinity, and photoperiod, and used consistent rearing procedures (initial stocking density, feeding regime). However, all batches assigned to cluster B occurred after the end of October 1997. It is possible that an obscure or undocumented but detrimental change in rearing conditions or procedures took place at this time, but we are unable to determine what this might have been.

Variation in parental or egg quality is a possible explanation for the variation in behavior among batches. We obtained eggs for our laboratory experiment from four separate broodstock tanks, each containing 2 or 3 females and 2 or 3 males. Therefore, each batch was produced by an unknown number of parents, and different batches obtained from the same tank may have been produced by the same or different parents. Therefore, it is impossible to assess the role of genetics in the behavioral differences we observed or to make inferences about changes in an individual female's egg quality over time. Nevertheless, we do have evidence that reproductive seasonality may have had an effect on batch variability, and we discuss this possibility in order to identify an important topic for future research.

Our broodstock spawned voluntarily over a protracted reproductive season (5–9 months for any particular broodstock

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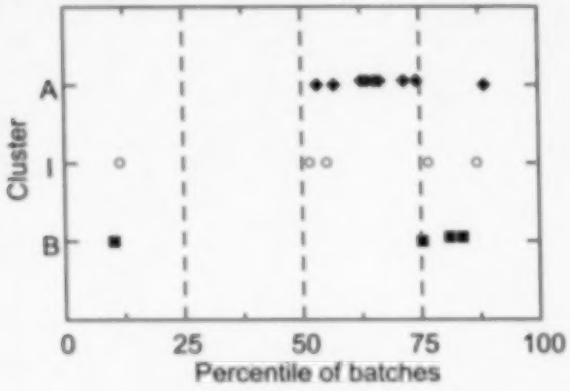
Fig. 7. Possible relationship between behavioral performance of batches of red drum larvae and timing of batch production within the spawning season. Relative timing is expressed as the ordinal rank of a batch divided by the number of batches produced by a tank of broodstock in a season. Fast- and slow-growing larvae within each batch are plotted separately. Batches in cluster A (◆) had better behavioral performance than batches in cluster B (■). Batches labeled I (○) had intermediate behavioral performance. Data shown are for nine batches; spawning data were not available for one batch.



tank) that was often out of phase with their natural spawning period (locally September and October, according to hatching dates of wild-caught larvae; Rooker and Holt 1997). Generally, spawning in a tank would begin at some point in the year and its frequency would increase over the next 3–5 months, then decrease before ceasing completely. Batches having poorly performing larvae (cluster B) were produced during the early and late stages of this reproductive period (that is, in the first and last quartiles of spawns). All but one of the batches in cluster A were produced during the third quartile of the spawns from a tank (Fig. 7). The lone exception was fast-growing larvae from batch 6, which were spawned at the end of the season (87th percentile of spawns). This apparent association between relative timing of a batch within the spawning period and behavioral performance of offspring may be the product of poorer maternal or egg quality at the start and end of the reproductive period. Several studies have shown that egg quality (e.g., diameter, dry weight, and energy, yolk, fatty acid, amino acid, or hormone content) can vary among batches with a peak at midseason (e.g., Kamler and Stachowiak 1992; Kjørsvik 1994; Chambers and Waiwood 1996), but links between egg quality and larval behavior have not been established. Browman et al. (2003) found no connection between maternal nutritional condition and routine swimming behavior of offspring in Atlantic cod (*Gadus morhua*), at least under non-extreme conditions.

In summary, we found that growth rates of red drum larvae were not related, positively or negatively, to predation-mortality rate or to performance of various survival skills. There were significant and coordinated differences among batches of larvae in the behavioral skills larvae could use to evade predators. Specifically, elevated responsiveness to threatening stimuli and improved timing and heightened magnitude of escape responses produced compounding benefits to the survival potential of some batches over others. The underlying causes of the variability among batches are not known, but seasonality of maternal or egg quality is a possible source of variation in larval behavioral performance. Understanding the causes of variation in larval antipredator behavior and their implications for larval-stage mortality and subsequent recruitment success is a critical area for further research.

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Oceanographic connectivity among marine protected areas on the north coast of British Columbia, Canada

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Abstract: The main objective of our study was to use a three-dimensional oceanographic simulation model to understand connectivity among the proposed Gwaii Haanas National Marine Conservation Area (GHNMCA) and 10 other proposed or existing marine protected areas (MPAs) on the north Pacific coast of Canada. The simulations were conducted using passive particles placed at three depths and vertically migrating particles for 30 or 90 days in late winter. Simulated surface particle dispersion was found to be consistent with winter ocean current observations made from analysis of satellite imagery, current mooring, and drifter data. The GHNMCA would contribute to a network of MPAs because it supplies and receives particles from other MPAs in northern British Columbia. Model simulations also indicate that the greatest source of particles to GHNMCA originate from 30-m and not 2-m flows. Finally, the simulated mean daily dispersal rate of 2.0 km·day^{-1} would allow fish and invertebrates to self-seed northern portions of the GHNMCA in winter. Together, the GHNMCA and other MPAs appear to contribute a large percentage of particles to non-MPA regions in northern Hecate Strait, which may be considered a particle sink in winter.

Résumé : L'objectif principal de notre étude est de comprendre, à l'aide d'un modèle océanique tridimensionnel de simulation, la connectivité entre l'aire marine nationale de conservation Gwaii Haanas (GHNMCA) et 10 autres zones marines protégées (MPA) actuelles ou proposées sur la côte pacifique nord du Canada. Les simulations se sont faites à l'aide de particules passives placées à trois profondeurs et de particules à migration verticale pendant des périodes de 30 ou de 90 jours en fin d'hiver. La dispersion simulée des particules en surface correspond aux observations des courants d'hiver faites au moyen d'imagerie satellite et aux données de courant provenant de bouées amarrées et dérivantes. L'aire GHNMCA contribuerait au réseau des MPA, car elle émet des particules vers les autres zones du nord de la Colombie-Britannique et en reçoit d'elles en retour. Les simulations du modèle indiquent que les courants à 30 m et non ceux à 2 m sont la source principale de particules pour GHNMCA. Enfin, le taux de dispersion moyen simulé de 2,0 km·jour^{-1} permettrait aux poissons et aux invertébrés de coloniser eux-mêmes les portions nordiques de GHNMCA en hiver. Ensemble, GHNMCA et les autres MPA semblent fournir un pourcentage important des particules aux régions qui ne sont pas des MPA dans le nord du détroit d'Hécate, qui peut être considéré comme un drain pour les particules en hiver.

[Traduit par la Rédaction]

Introduction

Parks Canada Agency is legally mandated with establishing a system of National Marine Conservation Areas (NMCAs) to represent the full range of marine diversity found in Canada's Atlantic, Arctic, and Pacific Oceans and the Great Lakes. NMCAs differ from terrestrial parks in that the marine areas will be managed for sustainable use without compromising the structure and function of the marine ecosystems, including the seabed and water column (Mondor and Mercier 1995). The major objective of the NMCA program is to select one area within each of 29 natural marine regions identified for Canada's coasts. Each NMCA must be representative of a natural marine region's marine biodiversity and geological, oceanographic, archaeological, cultural, and historical features.

One of the areas furthest along in the NMCA establishment process surrounds Gwaii Haanas National Park Reserve – Haida Heritage Site on the southern Queen Charlotte Islands, and it encompasses both the Hecate Strait and

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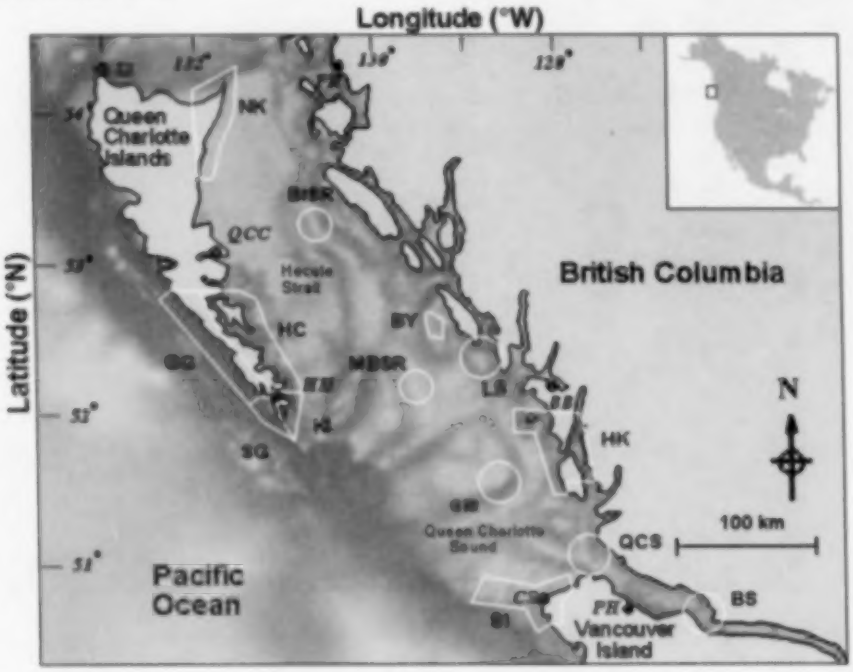
Fig. 1. Map showing the location of proposed and existing marine protected areas (MPAs) considered in this study. MPA abbreviations are as follows: NK, Naikoon Class A Provincial Park; GG, Gowgaia; HC, Hecate; BISR, Banks Island sponge reef; SG, Sgaang Gwaii; KI, Khunghit Island; BY, Byers, Conroy, Harvey, and Sinnett Islands Ecological Reserve; MBSR, Middle Bank sponge reef; LS, Laredo Sound; GIB, Goose Island Bank; HK, Hakai Recreation Area; SI, Scott Islands; QCS, Queen Charlotte Sound; BS, Blackfish Sound. Tidal stations are as follows: PR, Prince Rupert; BB, Bella Bella; QC, Queen Charlotte City; PH, Port Hardy; CS, Cape Scott; HH, Heater Harbour; LI, Langara Island.



Queen Charlotte Shelf Natural Marine regions of the Pacific coast of Canada. The Gwaii Hanaas NMCA (GHNMCA) is one of the few proposed or existing marine protected areas (MPAs) in British Columbia (Jamieson and Levings 2001), and it is expected to contribute to the sustainable use of natural resources. While the proposed GHNMCA may be representative of habitats or species, it is not apparent how it may function in a regional network of MPAs. A network may, for example, require that MPAs are suitable distances apart such that propagules produced by populations in one reserve replenish populations in other MPAs (Shanks et al. 2003). In addition, the functioning of the GHNMCA within a regional MPA network would require that marine plants and animals within the reserve have an impact on non-MPA areas (Palumbi 2001). Ultimately, the biological connectivity of an MPA results from the directed movement of juvenile or adult organisms or the interaction between ocean currents and smaller larval stages. The degree of connectivity generated by the latter process is a direct consequence of the suite of plants and animals found in various habitats (and their subsequent life history strategies; Grantham et al. 2003) and is a consequence of the regional oceanographic regime (Roberts et al. 2003).

In this study, we developed and used an oceanographic model to examine the connectivity of four regions within the proposed GHNMCA with 10 other MPAs in northern British Columbia. To facilitate our understanding of oceanographic connectivity, we tracked passive particles released in each MPA in late winter. It is during this period when high abundances of invertebrate and fish larvae are observed in the region (Fulton et al. 1982). Two main questions were addressed: (*i*) Is the proposed GHNMCA oceanographically connected to other northern British Columbia MPAs? (*ii*) Is the proposed GHNMCA self-seeding?

MPAs

On the northern coast of British Columbia, all of the existing MPAs are provincial, near shore, and small (Jamieson and Levings 2001). Below, we briefly discuss each MPA. Note that the MPA boundaries included in Fig. 1 are not legal boundaries and not to scale, but they are the particle seeding area boundaries used in the model to facilitate our understanding of connectivity. In this study, the northern most MPA we included is the Naikoon Class A Provincial Park (NK), which contains only a small marine area off the northeastern edge of the Queen Charlotte Islands. The Byers, Conroy, Harvey, and Sinnett Islands Ecological Reserve (BY) on the eastern side of Hecate Strait encompass about 118 km^2 of marine area. We also included the Hakai Recreation Area (HK) that contains about 570 km^2 of marine area in the eastern portion of Queen Charlotte Sound (Fig. 1).

In the southern portion of the study area, there are three federal government proposals for future MPAs. The Cana-

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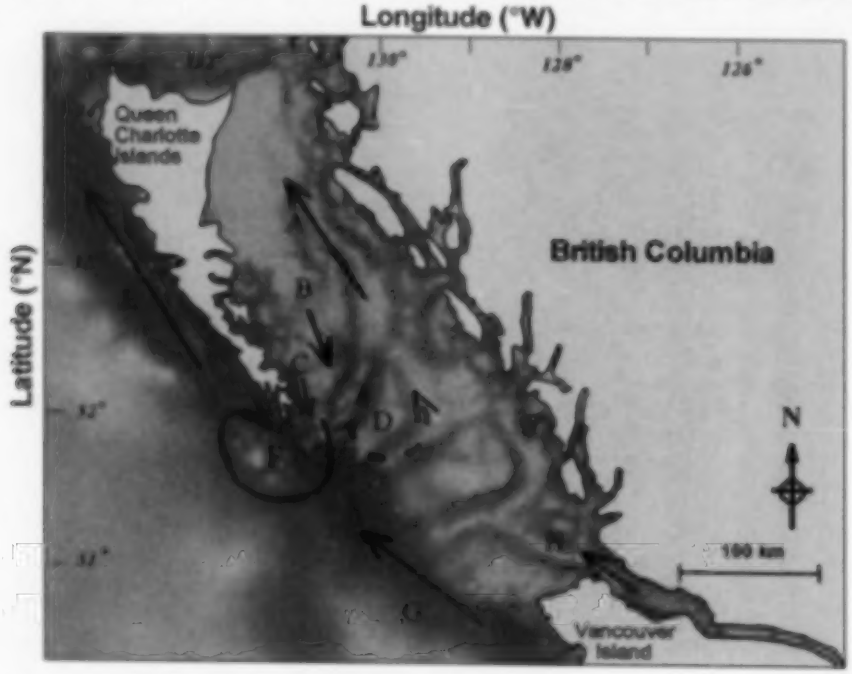
Fig. 2. Schematic of major ocean currents observed on the northern British Columbia coast in winter. Arrows indicate general direction of the following flows or currents. A, northerly flow through Hecate Strait; B, southward return flow; C, tidal mixing area; D, Middle Bank eddy area; E, Haida Current; F, Cape St. James mixing area; G, Davidson Current; H, Johnstone Strait outflow.



dian Wildlife Service has identified a region surrounding the Scott Islands (SI) as a possible migratory bird sanctuary (Scott Islands Marine Wildlife Area). There are no definitive boundaries for this region yet, and we arbitrarily enclosed a sea area around the northern tip of Vancouver Island (Fig. 1). Parks Canada Agency in the mid-1990s initiated a study to identify possible marine areas for a future NMCA feasibility study. The selection process has stalled, but we used the four original areas selected by Parks Canada that are thought to be representative of the Queen Charlotte Sound Natural Marine Region. At best, only one of these regions may become a future NMCA: Blackfish Sound (BS), Queen Charlotte Strait (QCS), Goose Island Bank (GIB), and Laredo Sound (LS). In Hecate Strait, Fisheries and Oceans Canada is implementing measures to preserve sponge reefs found at depths of 100–200 m. We included two general areas of possible sponge reef protection in the modeling study: Banks Island Sponge Reef (BISR) and Middle Bank Sponge Reef (MBSR; Fig. 1).

The proposed GHNMCA is about 3500 km^2, with the proposed boundaries extending about 10 km from shore (Fig. 1). The size of the GHNMCA and the complexity of oceanographic conditions allow us to divide it into four regions. We divided the east coast into two areas, Hecate (HC) to the north and Kunghit Island (KI) to the south, using Houston-Stewart Channel. KI experiences intense vertical tidal mixing, especially around Cape St. James. The west coast of GHNMCA was also divided into two regions. North of Houston-Stewart Channel, the region is called Gowgaia (GG), while the southwestern portion of the proposed GHNMCA, another region of high tidal mixing, is called Sgaang Gwaii (SG).

Oceanographic setting

The major winter currents observed in the study region are summarized in Fig. 2 and are derived from published studies analyzing satellite imagery, current mooring, and drifter data. In the Hecate Strait – Queen Charlotte Sound region, it is generally accepted that coastal winds, and to a much lesser extent runoff, are the major factors determining the non-tidal circulation over the continental shelf in winter (Thomson 1989). Winds primarily from the southeast or south force oceanic water into Queen Charlotte Sound, resulting in downwelling and mixing of warmer surface oceanic waters to the seabed. The winter water column, from mid-November to mid-April, is almost homogeneous to 200 m, with temperatures of 5–7 °C (Crawford and Thomson 1991; Jardine et al. 1993). In a nearly homogeneous water column, the internal Rossby radius of deformation, which determines the cross-strait scale of currents, is much less than the width of Hecate Strait (Crawford and Thomson 1991). Hence, there is no significant across-Strait current flow in winter, and the southeasterly winds mainly result in a strong northwesterly water flow along the eastern side of Hecate Strait (A in Fig. 2).

The constant flow of water northward results in a rise in sea level at the north end of Hecate Strait and a southward return current along the east coast of Gwaii Haanas (B in Fig. 2). This southward flow becomes relatively strong by the time it flows past Cape St. James, within 12 km of shore

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(see Fig. 8 in Crawford and Thomson 1991; Crawford et al. 2002). The southward flowing current is also enhanced by tidal rectification (C in Fig. 2; Crawford and Thomson 1991). To the southeast of the Queen Charlotte Islands, Crawford (1996) hypothesized that in winter, a counter-clockwise eddy is formed over the northern portion of Middle Bank (D in Fig. 2).

Off the west coast of the Queen Charlottes Islands, there is limited knowledge of the physical oceanography in winter. Thomson and Emery (1986) did, however, describe a narrow (20–30 km wide), northward-flowing current along the continental slope of the northern shelf in winter (E in Fig. 2). The Haida Current typically extends northward along the coast of the Queen Charlotte Islands, flowing more than 200 km towards the southern Alaskan Pandhandle (Thomson 1989). The current is attributed to alongshore wind stress and surface sea slope. Satellite imagery, in situ sampling, and model simulations have recently shown that eddies are regularly found to the southwest of Cape St. James in winter (F in Fig. 2). These eddies are formed (Crawford et al. 2002; Di Lorenzo et al. 2005) when the mean advection of warmer fresher water around the Cape from Hecate Strait generates plumes of buoyant flow, which intensify and sustain small patches of anticyclonic circulation immediately to the northwest of the cape. When the flow is strong, several of these smaller eddies can merge to generate a larger feature, the Haida Eddy. The Davidson Current (G in Fig. 2) is also known to extend northwards along the continental shelf from Vancouver Island, across the mouth of Queen Charlotte Sound. Finally, ocean currents in the winter flow out of Johnstone Strait northward into Queen Charlotte Sound (H in Fig. 2).

Methods

Oceanographic model

Apart from the eddy formation study of Di Lorenzo et al. (2005), previous modelling in the region has generally focused on the circulation resulting from either tidal (Thomson and Wilson 1987; Foreman et al. 1993; Cummins and Oey 1997) or wind forcing (Hannah et al. 1991; Crawford et al. 1999). In particular, Crawford et al. (1999) compared surface drifter tracks with two model simulations in Queen Charlotte Sound and concluded that when prevailing currents (i.e., those due to the tides or buoyancy forcing) are weak and local wind forcing is strong, surface currents may be predicted reasonably well by using wind data alone.

In this study, we used for our simulations the finite volume – finite difference oceanographic model, ELCIRC, developed at the Oregon Health and Science University by Baptista and coworkers (Zhang et al. 2004). It solves three-dimensional hydrodynamic equations for velocity and surface elevation and three-dimensional transport – diffusion equations for salinity and temperature in the presence of turbulent mixing. The domain has a variable resolution with, in this case, triangle sides ranging from 400 m near Cape St. James to 40 km west of the continental shelf. The model is forced with tides and winds and is initialized with salinity and temperature fields that were constructed from historical observations. Throughout all model runs, these fields were strongly nudged (with depth-dependent weights) back to their initial conditions. At the surface, the nudging had an e-folding time scale of approximately 1 hour. Although there was no direct surface heat flux, the foregoing nudging ensures that near surface temperatures remained close to their seasonal averages.

As with prognostic, finite element models such as QUODDY (Lynch et al. 1996), ELCIRC allows the flexibility of variable resolution to provide a better representation of the complicated coastline and bathymetry found in northern British Columbian waters. However, unlike QUODDY, ELCIRC has other attributes (e.g., Eulerian–Lagrangian time stepping, local volume conservation, and level, rather than terrain-following surfaces, in the vertical) that make it more accurate, efficient, and computationally robust. ELCIRC also permits the choice of several mixing schemes, including the popular Mellor–Yamada 2.5 closure scheme (Mellor and Yamada 1982) that has been selected here. A more complete description of the model and its performance in a series of test problems can be found in Zhang et al. (2004).

Our model domain ranges between 45°N and 59°N latitude and extends to approximately the 3500-m depth contour offshore. There are 42 level surfaces in the vertical, with resolution as fine as 0.5 m near the surface to provide an accurate representation of wind mixing. Tidal forcing along the model boundaries was provided by interpolating surface elevation amplitudes and phases from a larger model for the northeast Pacific Ocean (Foreman et al. 2000*a*). Eight tidal constituents (the four largest semidiurnals and diurnals), comprising approximately 85% of the total tidal range, were included in the simulations. Wind forcing was taken from observations at a network of Environment Canada offshore buoys, and this will be described in more detail later. Finally the initial three-dimensional fields of salinity and temperature were computed from historical observations going back as far as the 1940s and processed in a manner similar to that described in Foreman et al. (2000*b*). In this case, only winter observations were employed. The longer-term evolution of the temperature, salinity, and wind fields determine the non-tidal background flows.

Particle experiments

The main purpose of the particle experiments was to understand the potential oceanographic connectivity of the proposed GHNMCA with other regions. To give the particle experiments some realism, we used the literature to guide our selection of simulation time period, simulation duration, and depths studied. A cursory review of the primary literature for 44 species of fish and 22 species of invertebrates present in the proposed GHNMCA identified February to April as an important period, with high abundances of fish and invertebrate larvae. Recent work by Grantham et al. (2003) and Shanks et al. (2003), respectively, indicated that a typical larval duration for marine invertebrates is about 30 days, while for west coast fish it is about 90 days. Some invertebrates have relatively short pelagic larval phases (e.g., northern abalone), but we have not considered particles with short dispersal times or particles that remain near the seabed, because we are interested in properties that would have the highest potential to connect MPAs.

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Because pelagic invertebrate and fish larvae are found at different depths in the water column, we seeded particles in each MPA at depths, relative to the surface, of 2 and 30 m. We also investigated the movement of particles at 100 m for seven of the MPAs (not all MPAs contained waters with 100-m depth). The absolute particle seeding elevation ultimately varied depending on the local height of the surface at the seeding time and the location of insertion. The 2-, 30-, and 100-m groups were constrained to maintain a constant vertical distance from the surface and are subsequently referred to as the upper, middle, and lower particle groups. Particles were allowed to touch the bottom, but would refloat on a rising tide when the vertical distance to the surface increased above their preset depth. Grounding was rare and temporary. There were no grounded particles at the end of any of the model runs.

We also included a generic particle with vertical migratory behavior meant to mimic fish larvae such as *Pleuronectes vetulus*, *Pandalus danae*, and some *Sebastes* spp. The particles were inserted at 5 m below the surface and followed a vertical migration pattern that kept them near the surface overnight and at 40 m during the day. The particles descended between 0600 and 0700 local time and rose again between 1800 and 1900. If the bottom was less than 40 m, then the particles remained at 2 m above the bottom during the daytime.

Particle seeding was constrained to the boundaries of the proposed and existing MPAs depicted (Fig. 1). Particles of each group were released at random locations within each area at 3-day intervals to avoid spatial and tidal bias in the analysis.

Wind field scheduling

Climatic wind fields were generated based on the Faucher et al. (1999) reanalysis of the 6-h buoy winds. Our first choice would have been to run with all 40 years of wind data; however, we estimate that would have taken a minimum of 120 days of CPU time over a period of 180 days and thus was prohibitively expensive. The method we discuss below avoided the highly subjective process of choosing a subset of years. It also avoided all of the problems associated with time series and vector averaging. An unsupervised neural network Kohonan classifier was used to identify 32 wind classes for the time of year of interest from 41 years of Faucher winds. No assumptions or conditions were imposed on the classifier other than the number of classes. Initially the classes were assigned random locations within the n-dimensional space of the classifier. In our case, there were 27 dimensions representing the month and the u and v wind components at the 13 weather buoys located within the model domain (see Fig. 1). We classified wind observations by comparing the observations with each class and selecting the class that is nearest to the observations in the 27-D classification space. The network learns by nudging the class in the direction of the wind state. The process is iterative and continues until the number of wind states that change class in iteration reaches a steady state. Tables were then built giving the probability of each class of wind being followed any other given class of wind.

To schedule a wind field, we generated a random number and used as an index to look up the starting wind. The remaining winds were scheduled via a Markov Chain, where random numbers were used as indices in the probability tables to pick the next wind class in the chain. The Markov Chain was set up so that we would only schedule winds from a class that had followed the current class at some time in the observed winds. It is possible that there will be some very unlikely wind situations when a wind at one extreme of a class is followed by a wind at some extreme of the following class. This may introduce some random error into the simulations, but it should not result in a systematic bias, since all choices were based on probability distributions; thus unusual occurrences should be rare. Within the class, the random number was used to select the actual winds to schedule. This technique schedules winds that are consistent both spatially and temporally. Spatial integrity is maintained by scheduling winds that have actually occurred at the buoys at some time in the 41-year reanalysis period. Temporal integrity is maintained by the Markov Chain that schedules classes of winds in sequences that have actually occurred in the record according to the sequence probability.

A Monte Carlo approach was used to select schedules that were most similar to the 40-year average winds for the time of year being modelled. 10 000 schedules were generated and the one with the lowest average root mean square error (RMSE) with the offshore weather buoy mean wind was selected to force the circulation model. This average RMSE was typically between 0.2 and 0.1 $m \cdot s^{-1}$ for 1-month periods and less than 0.1 $m \cdot s^{-1}$ for 3-month periods. The average RMSE of variance was typically 1–2 $m \cdot s^{-1}$.

The periods of interest that were scheduled for analysis were the 3-month period February–April (90-day simulation) and the month of April (30-day simulation). Four February–April winds were scheduled and eight April winds were scheduled. We present model results from the average of these simulated replicates.

Particle movement

Particle movement was derived from the ELCIRC velocity field. At each time period, the water velocities at the particle location were interpolated from the finite volume velocity field. Change in velocity, or acceleration, was calculated from the previous period. A half-period position was then determined using the velocity for the half period and temporal acceleration for the full period. For the second half of the period, acceleration was determined from the change in velocity between the start of period position and the half-period position. The final particle position was calculated using the velocity for half the period and the spatial acceleration for the whole period.

$$s_{1/2} = s_0 + (v_{0,T})t/2 + (v_{0,T} - v_{0,T-1})t$$

$$s_1 = s_{1/2} + (v_{1/2,T+1/2})t/2 + (v_{1/2,T+1/2} - v_{0,T})t$$

where s_T is position at period T, t is time interval, and $v_{s,T}$ is velocity at position s and period T.

The particle movement algorithms were developed to fit within the constraints and error limits imposed by embedding the particle code within the ELCIRC code. We tested the algorithms by imposing a steady state velocity field on ELCIRC (by substituting our velocities at each location at each step). We then compared out-particle trajectories to

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Table 1. Observed and calculated M_2 (lunar semidiurnal) and K_1 (luni–solar diurnal) elevation amplitudes (amp; cm) and phase lags (degrees, UTC (Coordinated Universal Time)) for the seven sites in Fig. 1.

	M_2				K_1			
	Observed		Model		Observed		Model	
Site	amp	phase	amp	phase	amp	phase	amp	phase
Prince Rupert	195	267	196	279	51	259	52	256
Bella Bella	130	250	135	253	46	252	44	247
Queen Charlotte City	197	272	182	281	51	262	49	263
Port Hardy	133	252	134	257	50	250	46	249
Cape Scott	108	244	111	244	44	246	44	242
Langara Island	119	261	125	264	47	257	49	253
Hecate Harbour	119	264	115	267	44	258	44	253

stream traces in a commercial postprocessing product (Tecplot). In a simple rotating field, the particle tracks did not diverge from the stream traces after 10 rotations. In more complex fields (egg rotation with accelerating, three-dimensional translations), the particle tracks did not diverge from the stream traces after hundreds of time steps (3 days with 5-min time steps). Only with very high velocities (tens of metres per second) did the system diverge from stream traces.

Model runs

Each simulation run consisted of a model run-up period followed by a seeding interlude and a run-down period. The run-up period allowed time for the ELCIRC model to establish representative water conditions. During the seeding interlude, five sets of particles were added to the model at 3-day intervals spanning one 15-day tidal cycle. The run-down period tracked the particles until the last seeded group had been in the water for the required analysis interval. Four February–April runs were made, yielding 20 sets of particles.

Results

We consider three aspects of the simulation modeling. First, we present how the model results compared favourably with historical tide gauge and current meter observations. Second, we discuss the simulation results in the context of connectivity of the proposed GHNMCA and other north coast MPAs. Third, we discuss general results about particle travel over 30 days and 90 days and three depths (2, 30, 100 m) and also about vertical migrators.

Model validation

Tidal elevations and currents can be decomposed into sinusoidal contributions (constituents), and the two of the most important along the British Columbia coast are the lunar semidiurnal (M_2) and the luni–solar diurnal (K_1) constituents, with approximate periods of 12.4 and 23.9 hours, respectively. M_2 has at least twice the elevation amplitude of all other constituents, including K_1. Analyses of model results demonstrated that the tidal fields compared favourably with historical data. Model and observed elevation amplitudes and phase lags for constituents M_2 and K_1 at seven tide gauge locations encompassing the region of interest are listed (Table 1). In general, the accuracy is seen to be very good, with a maximum amplitude error of <8% at Queen Charlotte City and a maximum phase error of about 25 min at Prince Rupert. One-hour discrepancies in the M_2 and K_1 phases are approximately 29° and 15°, respectively. Average amplitude and phase errors are 3% and 11 min, respectively. The contours of the vertically averaged, major semi-axis ($cm \cdot s^{-1}$) of the current ellipses for M_2 may be compared with Foreman et al. (1993, their Fig. 5), which also included values computed from current meter observations. Again, the accuracy is seen to be quite good.

The accuracy of model-generated background flows in Hecate Strait and Queen Charlotte Sound is more difficult to assess, particularly for the late winter period, where unlike summer, fewer observations have been made. Nevertheless, Freeland et al. (1984), Crawford and Thomson (1991), and Crawford et al. (2002) have shown some average winter currents. The seasonal temperature and salinity fields predominantly determine these average flows. Given that our initial model conditions have been computed from historical temperature and salinity observations taken in the winter and the fact that through nudging, the model does not allow significant departures from these values throughout the run, we are reasonably confident that these fields, and hence the associated currents, are representative of typical winter conditions. Furthermore, Zhang et al. (2004) evaluate ELCIRC wind-driven flows against an analytical test case and find them to be very accurate. Therefore, we are confident that component of the background flow is also quite accurate. The particles that we modeled were, for the most part, near the surface so that it was critical for the model to respond realistically to wind forcing. This was tested by subjecting the model to constant wind forcing and verifying that the model was able to produce wind-driven currents that followed the classic "Ekman Spiral" (Pond and Pickard 1978).

Finally, there was no explicit horizontal diffusivity in any of the model runs, but the semi-Lagrangian time stepping employed by ELCIRC did impart a spatially varying numerical dispersion. Though difficult to quantify, the accuracy of the tidal currents suggests that the precise values for this dispersion were not sufficiently large to affect other components of the current field.

MPA connectivity and particle retention

The simulated particle spread pattern for each MPA after 90 days for three depths and vertical migrators is shown (Fig. 3). We also include a matrix summarizing particle con-

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Fig. 3. (*a*) Simulated spread of particles after 90 days. Particles were seeded at one of three depths (2, 30, or 100 m) and vertical migrators (VM) for each of 10 marine protected areas. (*b*) Spread of particles seeded at one of three depths (2, 30, or 100 m) and VM for each of four regions in the proposed Gwaii Haanas National Marine Conservations Area. See Fig. 1 for definition of abbreviations.

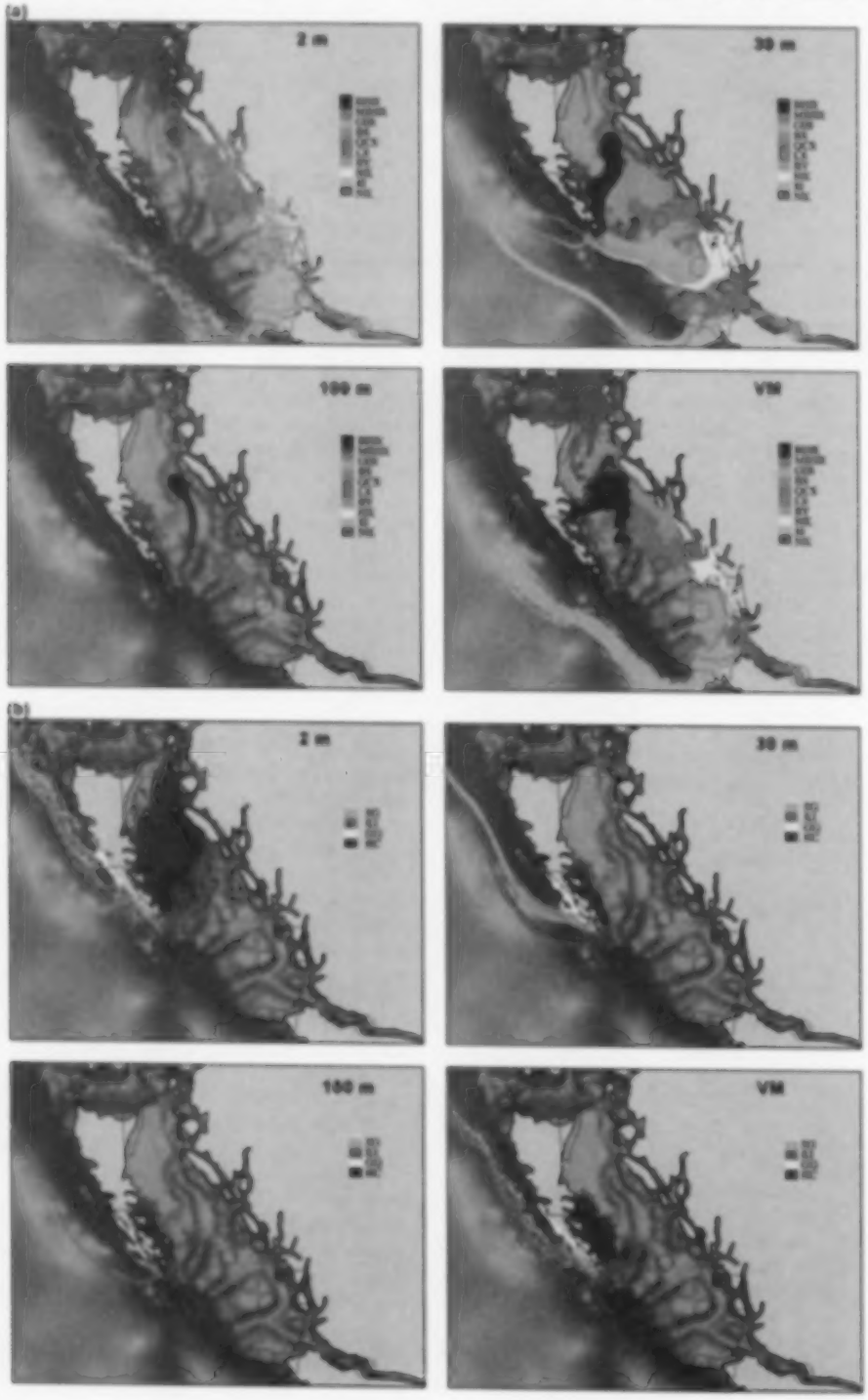

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Table 2. Connectivity matrix showing the percentage of particles released in a source marine protected area (MPA) (rows) and ending up in a sink MPA (columns) after 90 days (see Note below for example).

	NK	HC	GG	KI	SG	SI	HK	BY	LS	QCS	BS	GIB	MBSR	BISR
2 m														
HC	2	0	4	1	1	0	0	0	0	0	0	0	0	63
GG	0	29	0	0	13	0	0	0	0	0	0	0	0	0
KI	0	42	1	0	51	0	0	0	0	0	0	0	0	6
SG	0	0	81	19	0	0	0	0	0	0	0	0	0	0
NK	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BISR	30	0	0	0	0	0	0	0	0	0	0	0	0	0
BY	0	0	0	0	0	0	0	0	0	0	0	0	0	51
MBSR	0	0	0	0	0	0	0	31	4	0	0	0	0	64
LS	0	0	0	0	0	0	0	36	0	0	0	0	0	42
HK	0	0	0	0	0	0	2	0	32	5	0	7	0	2
GIB	0	0	0	0	0	0	63	0	33	0	0	0	0	3
QCS	0	0	0	0	0	0	60	0	18	0	0	22	0	0
SI	0	0	0	0	1	0	14	0	1	24	0	54	0	0
BS	0	0	0	0	0	0	0	0	0	40	0	0	0	0
30 m														
HC	0	34	6	17	40	0	0	0	0	0	0	0	0	0
GG	0	3	63	0	10	0	0	0	0	0	0	0	0	0
KI	0	9	0	0	90	0	0	0	0	0	0	0	0	0
SG	0	0	78	15	0	0	0	0	0	0	0	0	0	0
NK	12	0	0	0	0	0	0	0	0	0	0	0	0	0
BISR	0	9	0	21	70	0	0	0	0	0	0	0	0	0
BY	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MBSR	0	0	0	0	0	0	0	0	0	0	0	0	55	0
LS	0	0	0	0	0	0	0	0	0	0	0	0	100	0
HK	0	0	0	0	11	0	42	0	0	0	0	45	0	0
GIB	0	0	0	3	58	0	0	0	0	0	0	0	4	0
QCS	0	0	0	0	0	99	0	0	0	0	0	0	0	0
SI	0	0	0	0	0	5	0	0	0	0	0	0	0	0
BS	0	0	0	0	0	0	0	0	0	13	26	0	0	0
100 m														
HC	0	83	0	10	0	0	0	0	0	0	0	0	0	0
GG	0	0	75	0	2	0	0	0	0	0	0	0	0	0
KI	0	21	0	12	63	0	0	0	0	0	0	0	0	0
SG	0	0	75	18	1	0	0	0	0	0	0	0	0	0
NK	na	na	na	na	na	na	na	na	na	na	na	na	na	na
BISR	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BY	na	na	na	na	na	na	na	na	na	na	na	na	na	na
MBSR	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LS	na	na	na	na	na	na	na	na	na	na	na	na	na	na
HK	na	na	na	na	na	na	na	na	na	na	na	na	na	na
GIB	0	0	0	0	0	0	1	0	0	0	0	80	0	0
QCS	na	na	na	na	na	na	na	na	na	na	na	na	na	na
SI	na	na	na	na	na	na	na	na	na	na	na	na	na	na
BS	na	na	na	na	na	na	na	na	na	na	na	na	na	na
VM														
HC	0	10	7	17	18	0	0	0	0	0	0	0	0	0
GG	0	23	26	0	9	0	0	0	0	0	0	0	0	0
KI	0	14	0	0	86	0	0	0	0	0	0	0	0	0
SG	0	0	95	4	0	0	0	0	0	0	0	0	0	0
NK	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BISR	0	16	0	0	0	0	0	0	0	0	0	0	0	4
BY	2	0	0	0	0	0	0	0	0	0	0	0	0	62
MBSR	0	0	0	0	0	0	0	35	12	0	0	0	0	32

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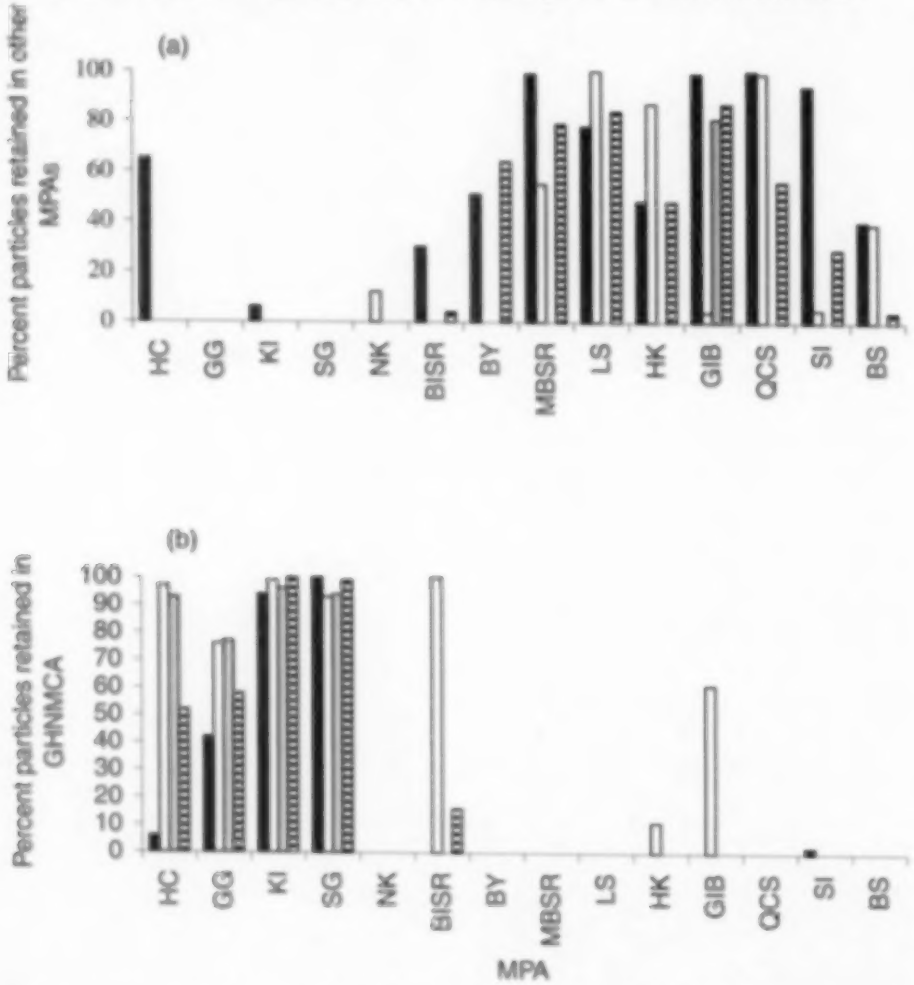
Table 2 (*concluded*).

	NK	HC	GG	KI	SG	SI	HK	BY	LS	QCS	BS	GIB	MBSR	BISR
LS	0	0	0	0	0	0	0	72	0	0	0	0	0	12
HK	0	0	0	0	0	0	29	0	18	0	0	1	0	0
GIB	0	0	0	0	0	11	76	0	0	0	0	0	0	0
QCS	0	0	0	0	0	31	25	0	0	0	0	0	0	0
SI	0	0	0	0	0	0	0	0	0	29	0	0	0	0
BS	0	0	0	0	0	0	0	0	0	4	0	0	0	0

Note: For example, 2% of particles released at 2 m from HC ended up in HK after 90 days. MPA abbreviations are as follows: NK, Naikoon Class A Provincial Park; GG, Gowgaia; HC, Hecate; BISR, Banks Island sponge reef; SG, Sgaang Gwaii; KI, Khunghit Island; BY, Byers, Conroy, Harvey, and Sinnett Islands Ecological Reserve; MBSR, Middle Bank sponge reef; LS, Laredo Sound; GIB, Goose Island Bank; HK, Hakas Recreation Area; SI, Scott Islands; QCS, Queen Charlotte Sound; BS, Blackfish Sound; na, not applicable because depths were <100 m.

Fig. 4. The percentage of particles released in one of 14 marine protected areas (MPAs) and retained in one of the 10 non-Gwaii Haanas MPAs (*a*) or one of four regions of the proposed Gwaii Haanas National Marine Conservations Area (*b*). 2 m, solid bars; 30 m, open bars; 100 m, shaded bars; vertical migrators, hatched bars. See Fig. 1 for definition of abbreviations.



nectivity of MPAs after 90 days. The rows in Table 2 are source MPAs, while the columns represent sink MPAs. The cells indicate the percentage of particles for a given depth that were retained within the sink MPA after 90 days. First, we present the general connectivity results for the proposed GHNMCA and other MPAs. Virtually no 2-m (surface) particles released in the proposed GHNMCA made it to other MPAs in the region (Fig. 4*a*). The only exception is that about 63% of HC and 6% of KI surface particles made it to BISR (Table 2). The majority of particles arriving in the

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Fig. 5. The percentage of particles released from different depths and from one of 14 study areas and lost to non-marine protected area (MPA) regions. 2 m, solid bars; 30 m, open bars; 100 m, shaded bars; vertical migrators, hatched bars. See Fig. 1 for definition of abbreviations.

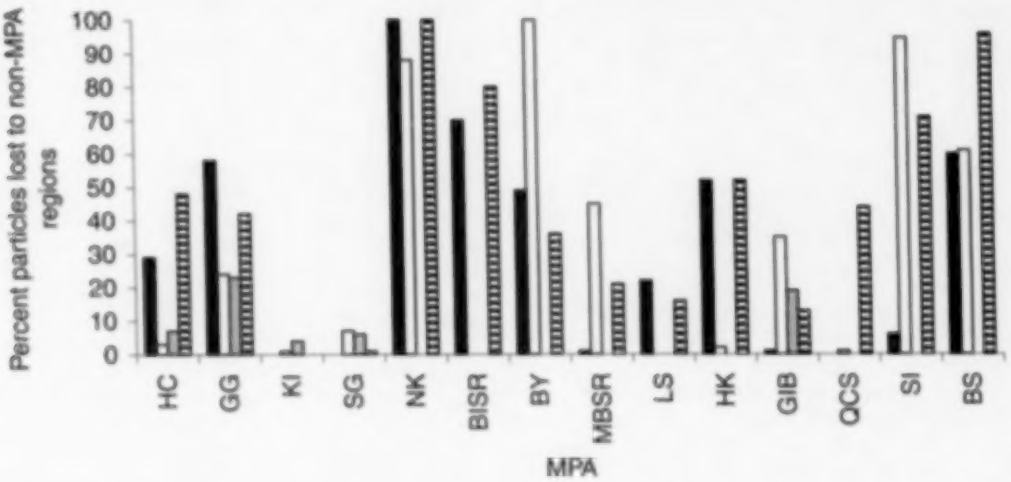
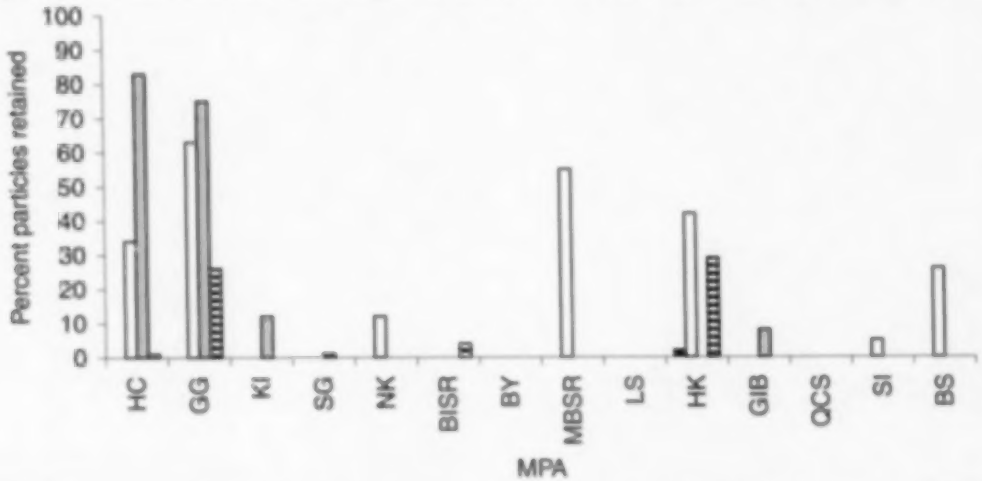


Fig. 6. The percentage of particles retained at each depth and marine protected area (MPA) after the 90-day simulation. 2 m, solid bars; 30 m, open bars; 100 m, shaded bars; vertical migrators, hatched bars. See Fig. 1 for definition of abbreviations.



proposed GHNMCA were not from other MPAs but from other regions of the GHNMCA. Only 1% of SI surface particles reached the GHNMCA. In contrast, 100%, 61%, and 11% of the 30-m particles from BISR, GIB, and HK, respectively, made it to the proposed GHNMCA (Fig. 4*b*).

An examination of particle loss from each region of the GHNMCA to non-MPA areas indicates that HC and GG had a higher percentage of particles lost at any depth compared with KI and SG. Regions in the GHNMCA lost relatively few particles to non-MPA areas compared with NK, BISR, HK, SI, and BS. Vertically migrating particles frequently had higher losses to non-MPA areas than losses of particles from 2 or 30 m (Fig. 5).

Self-seeding is defined as the percentage of starting particles remaining within the boundary of the home MPA after the 30- or 90-day simulation period. As expected, particle retention was higher for 30 days compared with the 90-day simulations and higher for 100 m versus the 2-m simulations. Note that not all MPAs had 100-m simulations because the maximum depth was <100 m. For the proposed GHNMCA, HC and GG had the highest self-retention of 30- and 100-m particles. The percentage of particle retention at 30 m for HC and GG was comparable with MBSR, HK, and BS (Fig. 6).

Particle travel

The model recorded two distances of particle movement: cumulative distance (m) travelled by a particle and the direct distance from seeding location to the end of travel (EOT). The latter was found to be, on average, about 12%–18% of the former depending upon seeding depth, and we present results below based on EOT distances. For all MPAs, parti-

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cles released in the surface mixed layer (2 m) for 90 days travelled, on average, 2.0 km·day^{-1} compared with 1.8 km·day^{-1} for particles at 30 m, 0.3 km·day^{-1} at 100 m, and 1.4 km·day^{-1} for vertical migrators. At 2 m, GG and SG had the greatest average daily particle movements of the 14 MPAs, totalling more than 400 km travelled in 90 days. Particles released at 30 m for six MPAs (SG, KI, GISR, HK, SI, QCS) were found to have higher average daily transports than particles released at 2 m. Thirty-metre particles at four of these MPAs were found to travel more than 200 km in 90 days. Particles were only released at depths of 100 m at seven MPAs, and particles at five of these MPAs travelled <30 km from their seeding locations. Particles given a vertical migratory behaviour were found to travel, on average, about 1.4 km·day^{-1}, with SG, KI, GG, and SI travelling more than 1.8 km·day^{-1}. In the proposed GHNMCA, HC had the lowest average daily particle movements at any depth of the four regions considered.

For all MPA sites combined, we measured distances (km) between the centers of each MPA site and compared these distances to the percent particles passing through each pair of MPA sites. The maximum recorded distance between MPAs where particles passed through was 364 km (1% of 2-m particles from SI passed through SG). The next highest connectivity distance was 219 km for 11% of HK particles at 30 m that passed through SG. The remaining connectivity distances were <180 km, and the majority of connections occurred at distances <60 km. Of the 11 pairs of MPA sites that were within 60 km of each other (center to center), about 50% of all possible depth–site combinations (22) had particles passing through.

Discussion

Connectivity among MPAs is one of the most poorly understood aspects of MPA function (Palumbi 2001). In this study, we developed and used an oceanographic model to examine the connectivity of the proposed GHNMCA with other proposed or existing MPAs along the north Pacific coast of Canada. An important factor influencing our conclusions is how well the model results reflect oceanographic reality. To this end, we demonstrated that the model has provided a reasonably accurate representation of tidal elevations and flows in Hecate Strait and Queen Charlotte Sound. We also argue that through the use of historical temperature and salinity observations, as both initial and restoring conditions during our runs, the background flows associated with these fields should be representative of typical late winter conditions. Finally, model validations performed by Zhang et al. 2004) indicate that our wind-driven flows should also be reasonably accurate.

We can also qualitatively compare our simulation results with observations of the major oceanic currents expected in this region in winter. On the basis of observed surface flows, we would have expected surface particles from the eastern GHNMCA to head mainly northward into central and northern Hecate Strait. Simulation results confirm that most HC and KI surface particles spread out from the eastern GHNMCA coast and move into the central and northern Hecate Strait. Some particles made it to Dixon Entrance. About 50% of the simulated surface particles released at KI moved south and west to SG, as expected, because of the year-round southward flow. About 29% of GG surface particles moved to HC after 90 days. These particles moved against the observed northerly flow on the west coast and also against the near shore southerly flow east of Cape St. James. This movement from GG to HC is against the average background surface flow and is likely due to short-term reversals in the predominantly northward winds and the strong tidal currents found in the SG and KI regions.

Surface particles released on the western coast of Gwaii Haanas primarily moved northward. The simulated particle flow was found to be very narrow, compared with the broader dispersal of surface particles in Hecate Strait. The narrow particle flow is likely due to the Haida Current observed (and modeled) off the west coast of the Queen Charlotte Islands (Thomson 1989). The vast majority of particles from other MPAs in Queen Charlotte Sound moved northward toward and through the eastern portion of Hecate Strait, and their movement is consistent with the eastern Hecate Strait flow observed in the region in winter (Crawford and Thomson 1991).

Given the qualitative evaluation of model results discussed above, we now present an overview of the simulation results that address our two major questions. The first question was the following: Is the proposed GHNMCA connected to other MPAs in northern British Columbia? One of the main roles of an MPA is to act as a source of eggs and larvae for surrounding areas (Roberts et al. 2003), and even a small flux of larvae to surrounding areas may help to maintain genetic flow between separated populations (Shanks et al. 2003). A major result from the simulations is that the GHNMCA could contribute particles to the two northern most MPAs (BISR and NK). In addition, it is likely that a small flux of larval particles from the west coast of the GHNMCA could pass near the Bowie Seamount, a proposed Fisheries and Oceans Canada MPA, located 180 km west of the Queen Charlotte Islands in the northeast Pacific Ocean at 53°18′N, 135°39′W.

The proposed GHNMCA may itself receive only a small flux of surface particles from the Scott Islands (SI) because of the northward-extending Davidson Current. It is possible that the strong northward-flowing current on the eastern side of Hecate Strait, and perhaps the Middle Bank Eddy, act as barriers to surface particle movement from southern MPAs in Queen Charlotte Sound towards the proposed GHNMCA. However, the model indicates that the GHNMCA would receive a higher flux of 30-m particles from three southern MPAs. The presence of this subsurface source of particles could only be determined from the oceanographic modeling and not from extrapolation of surface currents from satellite imagery. Ultimately, the dual function of receiving and distributing a small flux of particles suggests that the GHNMCA could serve an important role in maintaining the flow of regional, genetic biodiversity. This type of exchange is analogous to the stepping-stone genetic model, whereby populations exchange propagules only with adjacent populations, and these adjacent populations subsequently link populations furthest apart (Palumbi 2003).

Shanks et al. (2003) point out that a population that receives only a small flux of larvae to maintain gene flow may not receive enough larvae to sustain adult populations.

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Hence, another role of larval dispersal in an MPA is to sustain nearby populations with a larger number of new recruits. Our model results indicate that a high percentage of surface particles were dispersed from the proposed GHNMCA to non-MPA regions in central and northern Hecate Strait and along the west coast of the Queen Charlotte Islands. Northern Hecate Strait (e.g., Banks Island) also received a high percentage of particles from several other Queen Charlotte Sound MPAs, indicating that this area may be a sink for larvae and could be sustained from regions as far as a several hundred kilometres to the south. Crawford and Jamieson (1996) noted that drift cards released in winter off southern Vancouver Island arrived in northern Hecate Strait and Dixon Entrance 1 month later. Presumably the cards were carried northward in the Davidson Current, entrained into Queen Charolotte Sound, and moved northward along the east coast of Hecate Strait. Additional modeling and field work will be required to fully understand the role of the proposed GHNMCA and other MPAs in sustaining coastal populations in northern Hecate Strait.

The second major question addressed in this study was the following: Is the GHNMCA self-seeding? We defined self-seeding as the occurence of a particle within its home MPA at the end of a simulation. The simulation results indicated that two of the four GHNMCA regions (HC and GG) had high particle self-retention, especially at depths >30 m. Interestingly, both KI and SG exhibited relatively low particle retention at 30 m and 100 m compared with HC ad GG. This difference could be due to higher tidal mixing of deeper particles to the surface at KI and SG and then subsequent dispersal to HC and GG (Crawford 1996). Conversely, relatively low tidal mixing in HC and GG resulted in higher particle retention at 30 m and 100 m. Each region of the GHNMCA exhibited low surface particle retention. This may be because we used particles with long dispersal periods (90 days) and because the size of each region within the GHNMCA is too small relative to self-seeding potential.

Botsford et al. (2003) suggested that for an MPA to be self-seeding, it must be as large as the mean larval dispersal distance of organisms in the reserve. Our simulated mean daily dispersal rate of 2.0 km·day^{-1} for 2-m particles is similar to estimates made from empirical observations of larval plants, invertebrates, and fish. For example, from Fig. 1 in Shanks et al. (2003), we estimate that organisms with planktonic durations of 90 days had maximal dispersal distances of about 200 km (or 2.2 km·day^{-1}). Shanks et al. (2003) also plot the distances assuming a passive dispersal with a mean ocean current speed of 10 cm·s^{-1} (about 600 km or 6.7 km·day^{-1}) Our simulated average daily dispersal rate compares better with observed rates in Shanks et al. (2003) than it does with rates calculated using mean ocean current velocities. In our study, we found that the end of travel distances were about 15%–18% of total cumulative travel distances, indicating that particles travel in tidal cycles and other large-scale features (e.g., eddies) without great linear dispersal. Crawford and Jamieson (1996) modeled crab larvae dispersal in late winter in northern Hecate Strait and concluded that there is a basin-wide recirculating current in Dixon Entrance that retains larvae within the region until settlement.

Given our confidence in our mean particle dispersal rate, the model estimates that 2- and 30-m particles with a 30-day dispersal phase (e.g., invertebrates; Grantham et al. 2003) and particles with a 90-day dispersal phase (e.g., fish; Shanks et al. 2003) could disperse and be retained, on average, within 52–69 and 160–180 km from the source area, respectively. Because the boundary of the proposed GHNMCA is about 100 km long and because it runs parallel to the alongshore ocean current regime, it might be self-seeding for invertebrate and fish occurring mainly in the southern one-third of the reserve. It is unlikely that regions north of Burnaby Island would be self-seeding in winter for most invertebrate and fish species with long larval phases and larvae found in the top 30 m of the water column. An important caveat to this simulation result is that surface currents shift to a southward direction in summer (mid-June to mid-October; Jardine et al. 1993; Crawford 1996), and hence northern regions of the proposed GHNMCA may seed southern regions with fish and invertebrates species that release larvae into the water column at that time.

Overall, we found the three-dimensional oceanographic model to be an important tool for simulating the importance of tide and wind on the potential connectivity of the proposed GHNMCA with other regions on the north Pacific coast of Canada. It remains for the results of the model to be verified through detailed plankton sampling, including genetic studies, and to examine how connectivity may change over a variety of temporal scales through dynamic wind forcing.

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Distribution of Atlantic salmon (*Salmo salar*) postsmolts of different origins in the Bay of Fundy and Gulf of Maine and evaluation of factors affecting migration, growth, and survival

Gilles L. Lacroix and Derek Knox

Abstract: Atlantic salmon (*Salmo salar*) postsmolts surveyed by surface trawling in the Bay of Fundy and Gulf of Maine during 2001–2003 were aggregated in several areas in the Bay of Fundy and dispersed over a broader area in the Gulf of Maine. Postsmolt distribution reflected the major surface-current vectors and was independent of origin (wild vs. hatchery, inner vs. outer Bay of Fundy). Migration proceeded without disruption, and marked wild postsmolts from both the inner and outer Bay of Fundy were recaptured in the outer Bay of Fundy and the Gulf of Maine, where their distribution overlapped the commercial fishery for Atlantic herring (*Clupea harengus*). Marked postsmolts of wild origin were recaptured more frequently than those of hatchery origin but the overall density was low, and no schools of postsmolts were encountered that could offer protection from predators. Temperature and salinity in postsmolt habitat were favourable for growth and survival. Postsmolts were in excellent condition and had no bacterial or viral pathogens or salmon lice (*Lepeophtheirus salmonis*). They were feeding on pelagic prey (amphipods, euphausiids, and fish larvae) and the period of accelerated marine growth had started, indicating that environmental conditions and food supply were not limiting growth and survival.

Résumé : Des post-saumoneaux du saumon atlantique (*Salmo salar*) inventoriés au chalutage de surface dans le baie de Fundy et le golfe du Maine en 2001–2003 étaient rassemblés dans quelques points de la baie de Fundy et dispersés sur une plus grande surface dans le golfe du Maine. La répartition des post-saumoneaux correspond aux principaux vecteurs de courants de surface et elle est indépendante de leur origine (nature ou pisciculture, régions interne ou externe de la baie de Fundy). La migration s'est faite sans problème et les post-saumoneaux sauvages marqués provenant des régions interne ou externe de la baie de Fundy ont été capturés dans la région externe de la baie de Fundy et dans le golfe du Maine où leur répartition chevauche celle de la pêche commerciale du hareng atlantique (*Clupea harengus*). Il y a plus de recaptures de post-saumoneaux marqués d'origine sauvage que de post-saumoneaux de pisciculture, mais leur densité est faible et il ne semble pas se former de bancs de post-saumoneaux pour offrir une protection contre les prédateurs. La température et la salinité dans les habitats de post-saumoneaux sont favorables à la croissance et la survie. Les post-saumoneaux sont en excellente condition et ne portent ni pathogènes bactériens et viraux, ni poux du saumon (*Lepeophtheirus salmonis*). Ils se nourrissent de proies pélagiques (amphipodes, euphausiacés et larves de poissons) et leur période de croissance accélérée en mer est commencée, ce qui indique que les conditions environnementales et l'approvisionnement alimentaire ne limitent pas la croissance ni la survie.

[Traduit par la Rédaction]

Introduction

Information about Atlantic salmon (*Salmo salar*) during the postsmolt stage — from the time they leave the river until they reach oceanic feeding grounds — is sparse and difficult to acquire. Yet this period is often assumed to be a critical one for the marine survival and success of salmon populations (e.g., Friedland et al. 2000; Hansen et al. 2003). Trawling surveys in surface waters of the northeast Atlantic Ocean have captured salmon postsmolts and helped define the migration routes of some populations in coastal and oceanic habitat (Holst et al. 2000; Holm et al. 2003). In the northwest Atlantic Ocean, salmon postsmolts have been sampled from fisheries in the Labrador Sea and west Greenland area (Reddin and Short 1991; Reddin and Friedland 1993) and the northern Gulf of St. Lawrence (Dutil and Coutu 1988). Otherwise, little is known about the distribution and biology of postsmolts in coastal habitat and during early marine life.

A severe decline in the abundance of North American Atlantic salmon that has been attributed to decreased marine

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survival has resulted in the listing of some salmon stocks in the Bay of Fundy and Gulf of Maine as endangered (US Fish and Wildlife Service and National Oceanic and Atmospheric Administration (NOAA) 2000; Amiro 2003). Cairns (2001) outlined a wide variety of factors that have been hypothesized to reduce Atlantic salmon survival and cause this decline, but few of these have been tested, especially those acting during the early marine phase. Friedland et al. (2000) examined the growth of Atlantic salmon postsmolts and suggested that it may influence survival later in the marine migration. Stefansson et al. (2003) measured physiological changes in Atlantic salmon postsmolts during estuarine and coastal migration that may be advantageous for long-term marine survival. Rikardsen et al. (2004), reporting on the early marine feeding habits of Atlantic salmon postsmolts, considered that prey availability and feeding might influence postsmolt growth and survival. Lacroix et al. (2004) found that coastal habitat use (e.g., the presence of a weir fishery and the increase in predators near Atlantic salmon farms) could affect postsmolt survival.

This study reports the results of surveys conducted by trawling in surface waters of the Bay of Fundy and Gulf of Maine to capture live Atlantic salmon postsmolts and examine the following hypotheses related to their migration and survival. (*i*) Postsmolt migration was initially largely controlled by hydrography rather than by genetic, geographic, or rearing origin. (*ii*) Postsmolt migration was temporarily disrupted and survival potentially affected by unfavourable currents, temperature, or salinity in coastal habitat. (*iii*) Postsmolt habitat overlapped that of large commercially exploited fish stocks, increasing the likelihood of interception. (*iv*) Abundance of postsmolts was very low and they failed to form the large schools that could offer protection from predators. (*v*) Diseases or parasites endemic to Atlantic salmon farms in the Bay of Fundy infected migrating postsmolts and potentially affected marine survival. (*vi*) The rapid early marine growth phase important for postsmolt survival was affected by unfavourable habitat or failure to find suitable, abundant prey.

Methods

Trawling gear and fishing method

Atlantic salmon postsmolts were captured alive by trawling in the surface waters using methodology adapted from Holm et al. (2000) and Holst and McDonald (2000). An experimental postsmolt trawl (Åkrehamn Trålbøteri A/S, Åkrehamn, Norway) designed to sample a wide and shallow water layer at the surface was used for the first time in these surveys. The mouth of the trawl was shallow compared with that of pelagic trawls previously used in the other surveys, to target surface habitat where postsmolts have been found, and mesh sizes in the wings and fore panels were large and twine and rope diameters were small to reduce drag during rapid towing. The trawl was 122.5 m long, had a circumference of 236.8 m at the mouth, and had extra-long wings (59.4 m along the head rope) to maximize spread and the area fished at the surface. Trawl mesh sizes from the jib lines aft were 800, 400, 200, 120, 80, 60, 40, and 20 mm, but an 80 mm mesh liner that reached 1.2 m below the head rope was integrated into the central 29.2 m of the upper 800 mm mesh panel to reduce loss of postsmolts near the surface. The first bottom panel extended 10.4 m forward of the top panel at the mouth to help catch fish that sounded upon contact with the head rope.

The trawl was rigged for surface trawling by adapting the method of Valdermarsen and Misund (1995). Flotation was provided by 50 deep-water trawl floats (3.7 kg buoyancy each, 50-cm spacing) along the head rope, two round inflatable net buoys (combined buoyancy 720 kg) at each end of the head rope, and 8–10 low-drag inflatable net buoys (55 kg buoyancy each, 3-m spacing) in the centre section of the head rope. Main towing warps (18 mm diameter wire, maximum length 485 m), towing bridles (12 mm diameter wire, length 90 m), and 3-m^2 Thyborøn, Type 8 adjustable pelagic trawl doors (Thyborøn Skibssmedie A/S, Thyborøn, Denmark) were selected for lightness and rigged to spread the trawl at the surface with long warps. A 50-kg lead line on the foot rope with 50–60 kg weights suspended at each end was used to vertically open the trawl.

A light aluminum fish-holding tank (approximate volume 1000–1300 L) was attached to the trawl in lieu of a bag section to retain captured fish alive. It was rigged with 6–10 purse seine floats (3.7 kg buoyancy each) along each side to provide neutral buoyancy and add stability. The prow was designed to reduce drag and facilitate landing on the trawl ramp of the ship. An aluminum plate welded inside the tank near the top edge provided a covered holding space, and fish were channelled into the tank through a gap between the plate and the stern. The tank was brought on board full of water and fish were emptied through a gate valve into a holding tank on deck. Details of tank dimensions and design, material specifications, and methods of attachment to the trawl are available from the authors.

The CCGS *Alfred Needler*, a 50.3-m stern trawler with a main engine of 2600 kW was used in all surveys. The trawl was fished by setting as long a warp as possible without having the float line sink, to keep it well astern of the ship (warp length range 230–320 m). All trawling was done from the sea surface (i.e., head rope at 0 m) at about 4 kn (range 3.5–5.0 kn), and ship speed was adjusted to fish the trawl doors close below the surface. The ship towed in large arcs to keep the trawl out of its propeller wake, and prevailing currents were also used to help swing the trawl outside the wake. Minilog-TDX combined water temperature and depth loggers (Vemco Ltd., Shad Bay, Nova Scotia) were attached to the centre of the foot rope and to one of the trawl doors to monitor water temperature, the size of the trawl's vertical opening, and the depth of the door during fishing. The depth data were examined between tows, and adjustments to doors and weights were made when required. The depth of the holding tank during fishing was also occasionally verified and flotation was adjusted if necessary. Surface-water salinity was measured at each station between tows. Final warp length and other settings were recorded for each tow. The coordinates of the ship were recorded at the start and end of each tow, and trawling speed and water depth were recorded at 5-min intervals while fishing.

Survey areas and strategies

Fishing dates during the postsmolt surveys were 30 May to 13 June 2001, 26 May to 15 June 2002, and 4–18 June

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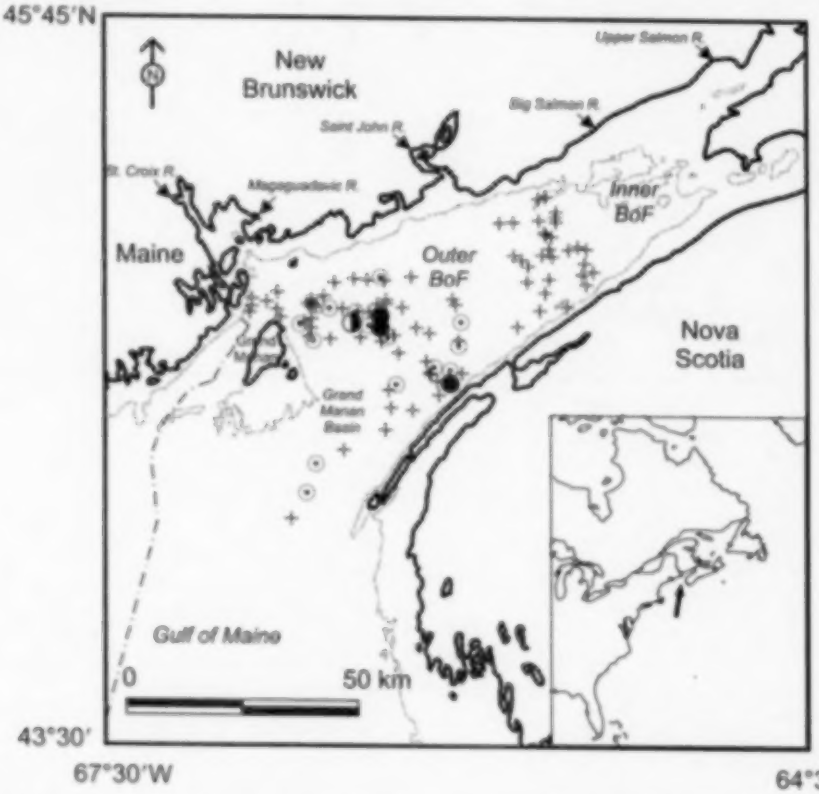
Fig. 1. Distribution and abundances (cross, 0 fish; solid circle within a circle, 1–5 fish; half-solid circle, 6–15 fish; solid circle, 16–30 fish) of Atlantic salmon (*Salmo salar*) postsmolts captured in 2001 during a survey in the Bay of Fundy (BoF) on the east coast of North America (inset). The 90-m isobath (·····), the International Maritime Boundary (— · — · —), and the five rivers where wild smolts were marked (arrows) are shown.



2003. These were selected to correspond to the time of peak smolt migration from rivers in the Bay of Fundy. In 2001, the strategy was to try to intercept postsmolts as they moved from the inner to the outer Bay of Fundy and then out into the Gulf of Maine, to identify migration corridors. The inner bay was that area extending into the bay north-northeast of the Saint John River, and the outer bay reached south-southeast from the Saint John River to the Grand Manan Basin (Fig. 1). These two areas were surveyed by trawling back and forth across the bay, each tow starting where the previous one ended, to fully cover the area. Each trawling site was fished for 1 h at an average speed of about 4 kn and covered approximately 6 km, and the starting point of the trawl haul was used for plotting coordinates.

In 2002, the area across the outer Bay of Fundy was surveyed as in 2001, but the survey was extended into the Gulf of Maine. A broader survey pattern was adopted to get overall coverage of the area extending between Nova Scotia and the International Maritime Boundary. Tows were made consecutively along transects oriented with the surface current flow or along north–south transects within the Gulf of Maine. Several transects were surveyed heading along southeastern Nova Scotia. Tow time was decreased to about 30 min in 2002 to reduce the possibility of postsmolt mortality from damage in the holding tank caused by the capture of large numbers of other fish. Speed was kept at about 4 kn and a distance of about 3.7 km was covered.

In 2003, the survey concentrated almost exclusively on broad coverage of the Gulf of Maine between Nova Scotia and the International Maritime Boundary. Tows were made mostly along north–south transects, and individual survey sites were farther apart (i.e., not continuous as in 2001 and 2002) and involved steaming for about 2.5 km between sites. Some sites along southeastern Nova Scotia just outside the 90-m isobath were also surveyed. A short tow time of about 30 min was again used, average speed was about 0.5 kn higher than in the previous 2 years, and a distance of about 4 km was covered.

Trawling was limited to daylight hours because of the presence in surface waters of large schools of Atlantic herring (*Clupea harengus*) throughout the areas surveyed and numerous spiny dogfish (*Squalus acanthias*) in several areas, starting at dusk and through the night. This was observed during experimental trawling conducted starting at dusk and during the night in 2000 and 2001, and the large catch size made surface trawling for salmon at night impossible (G.L. Lacroix, unpublished data).

Smolt marking

In each survey year, several thousand wild Atlantic salmon smolts that were captured migrating in several rivers

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Table 1. Numbers of Atlantic salmon (*Salmo salar*) smolts of wild origin marked and released in specific rivers of the Bay of Fundy and numbers marked and released from Canadian hatcheries in the Bay of Fundy during 2001–2003; percentages of wild and of hatchery-reared smolts are also shown.

	2001		2002		2003	
	n	%	*n*	%	*n*	%
Wild origin						
Upper Salmon River	24	1	105	3	0	0
Big Salmon River	623	24	438	14	841	36
Saint John River system	1 523	59	1 638	51	883	37
Magaguadavic River	365	14	890	27	515	22
St. Croix River	61	2	164	5	125	5
Total	2 596	100	3 235	100	2 364	100
Hatchery origin						
Bay of Fundy (common mark)	346 142	99	296 293	96	261 267	84
Bay of Fundy (river-specific marks)	5 117	1	13 217	4	16 266	5
Bay of Fundy (unmarked)	0	0	0	0	34 750	11
Total	351 259	100	309 510	100	312 283	100

of the Bay of Fundy, two of which were in the inner bay (Upper Salmon and Big Salmon rivers), were marked and released (Table 1). Their recapture at sea would provide river-specific information on migration route, distribution, and growth after several weeks at sea. The smolts were captured using rotary-screw fish traps (E.G. Solutions, Inc., Corvallis, Oregon) operated in each river from April to June. The smolts were sampled and then marked by jet injection of Alcian Blue dye (30 mg·L^{-1}, aqueous suspension) as described by Thedinga and Johnson (1995), using a needle-free MadaJet XL dental jet injector with reduced spring tension for fish tagging (Mada, Inc., Carlstadt, New Jersey). A mark that consisted of a small blue dot was applied to a different fin or lobe of the caudal fin for each river. Identical marks experimentally applied to juvenile salmon held in a hatchery in 2001 remained easy to recognize after 4 months (G.L. Lacroix, unpublished data).

Each year, more than 300 000 smolts reared in Canadian hatcheries were released in rivers of the Bay of Fundy for enhancement purposes (Table 1), the majority in the Saint John River system (89% in 2001, 81% in 2002, and 64% in 2003). Most smolts had been marked by clipping the adipose fin, but a small proportion also had a river-specific tag for identification, either a numbered Carlin tag or coloured plastic garment and streamer tags. Information about numbers of smolts marked and released in Canada was provided by the Department of Fisheries and Oceans (T.R. Goff, Mactaquac Fish Hatchery, 114 Fish Hatchery Lane, French Village, NB E3E 2C6, Canada, and S.F. O'Neil, Science Branch, Box 1006, Dartmouth, NS B2Y 4A2, Canada, personal communication). In addition, more than half a million smolts reared in US hatcheries in 2001 and 2002 and about half that amount in 2003 were also released for enhancement in rivers of Maine, most of which drain into the Gulf of Maine. In 2001 and 2002, about 38% of these smolts were marked and in 2003 they were all marked with coloured elastomer eye tags. Information about numbers of smolts marked and released in Maine was provided by NOAA-Fisheries (T.F. Sheehan, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543, USA, personal communication).

Postsmolt sampling

All fish captured were transferred from the trawl tank to large seawater tanks on deck, allowed to recover, and then sorted. Postsmolts were taken to a laboratory below deck, where they were held in a tank with flow-through seawater during sampling. Each postsmolt was individually handled after being lightly sedated using a clove oil solution (40 mg·L^{-1}). It was examined for the presence of external tags, specialized marks, and fin clips that could help identify its origin, presence/absence of fin erosion, presence/absence of scale loss, and presence/absence and abundance of ectoparasites such as lice. Fork length and weight were measured and a scale sample was taken. The fish were allowed to recover and, after regaining balance and darting behaviour, they were released back into the sea.

Salmon that died during capture had additional samples taken. The oesophagus, stomach, and intestine were removed and the contents were fixed in 10% formaldehyde for at least 1 month and then transferred to 70% ethanol. For each postsmolt sampled, food items were identified to the lowest possible taxonomic level and enumerated. The percentage of postsmolts with a specific food item and the percentage of food items falling within a taxon were determined.

Finally, the carcass less the digestive tract was placed in a sterile bag and immediately frozen. These samples were later examined by the Fish Health and Molecular Biology units of the Department of Fisheries and Oceans (Moncton, New Brunswick) for bacterial and viral pathogens. Tryptic soy agar and blood agar with and without 2% salt were used for culturing from the kidneys. The media would grow bacteria of a wide variety of genera, such as the fish pathogens *Vibrio* spp. (i.e., *Vibrio anguillarum* types I & II, *Vibrio salmonicida*, and other *Vibrio* species), *Aeromonas salmonicida*, *Yersinia ruckerii*, and others. The fish remains were assayed for possible viral fish pathogens, including the infectious salmon anaemia (ISA) virus, using salmon head kidney, chinook salmon (*Oncorhynchus tshawytscha*) embryo, and epithelioma papillosum cyprini cell lines incubated at 15 °C for 28 days. These cell lines would grow a variety of genera of viruses, including rhabdoviruses (e.g.,

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Table 2. Tow variables (mean ± standard deviation) for surface trawl hauls with and without Atlantic salmon postsmolts during 2001–2003 surveys in the Bay of Fundy and Gulf of Maine.

	2001		2002		2003	
	With salmon	No salmon	With salmon	No salmon	With salmon	No salmon
Number of tows*	19 (19)	81 (81)	51 (34)	104 (67)	23 (16)	120 (84)
Tow time (min)	56.1±6.79a	57.0±8.40a	34.7±11.0a	34.2±10.7a	32.6±8.64a	31.5±6.59a
Tow speed (kn)	4.08±0.14a	4.09±0.16a	4.08±0.20a	4.03±0.22a	4.62±0.17a	4.64±0.25a
Tow distance (km)	6.21±1.96a	6.05±2.33a	3.95±1.84a	3.62±1.20a	4.29±1.50a	3.93±1.11a
Trawl vertical opening† (m)	12.2±2.34a	13.2±2.11a	11.8±2.31a	11.9±1.85a	9.3±0.81a	9.1±1.48a
Surface temperature (°C)	7.1±0.60a	6.5±0.48b	8.7±0.69a	8.6±0.85a	8.2±0.90a	8.3±0.92a
Surface salinity (‰)	nd	nd	31.0±0.38a	30.8±0.58b	30.8±0.39a	30.8±0.48a

Note: Values within a row and year followed by a different letter are significantly different at $P \leq 0.05$ (independent-samples t test); nd, not determined.

*Numbers in parentheses are percentages.

†For 2003, the depth of the live holding tank at the cod end is reported instead of the depth of the trawl foot rope.

viral haemorrhagic septicaemia and infectious haematopoietic necrosis viruses) and birnaviruses (e.g., infectious pancreatic necrosis virus). Additionally, kidney samples were also assayed for the ISA virus using the reverse transcriptase polymerase chain reaction.

Scales collected from each postsmolt were cleaned, mounted on a slide, and examined first under a binocular microscope (magnification 64×). Images of individual scales were then scanned using a megapixel firewall digital camera and Image-Pro Plus 4.5 (Media Cybernetics, San Diego, California; image resolution 1280 × 1024). Stored images were examined and freshwater age was determined from annulus formation in the freshwater growth zone. The freshwater growth zone was also used to verify postsmolt origin (i.e., wild vs. hatchery). Hatchery-reared fish had a greater number of circuli than wild fish, and these were usually evenly spaced throughout the freshwater growth period without a clear winter annulus. In addition, only age-1 smolts were produced and released by hatcheries in Canada and Maine, whereas wild fish emigrated as age-2 and age-3 smolts. Initial growth intensity of postsmolts for the period until capture was then interpreted from the number and spacing of scale circuli, starting after the last winter annulus of the freshwater growth zone. The first spacing was measured between the first circulus of the postsmolt growth zone and the next circulus, and the spacing between all successive pairs was measured up to the outer edge of the scale, and new circuli were counted. Circuli were not counted and their spacing was not measured if an obvious winter annulus was not present, such as for many of the fish of hatchery origin. Scale measurements for each postsmolt were made using Image-Pro (resolution 0.002 mm per pixel) on a single scale representative of other complete (i.e., non-regenerated) scales on the slide and along a line drawn over the image bisecting the scale from the focus along the 360° axis of the scale as described by Friedland et al. (1996).

Other fish species

Many other species were captured near the surface, and they were identified, enumerated, and released alive. Those caught with salmon varied from year to year according to the area surveyed. The most common were lumpfish (*Cyclopterus lumpus*) (91%–100% of tows with salmon), alewife (*Alosa pseudoharengus*), Atlantic herring, Atlantic mackerel (*Scomber scombrus*), a variety of larval and age-0 fish, crustaceans (amphipods and euphausiids), ctenophores (comb jelly), and cnidarians (jellyfish). Fish larvae and age-0 fish were usually the most abundant, followed by Atlantic herring, lumpfish, and Atlantic mackerel. Fish were examined for ectoparasites, and many lumpfish carried the sea louse *Caligus elongatus* (51% in 2001, 32% in 2002, and 8% in 2003); mean densities of 4.3 (2001), 4.4 (2002), and 2.3 (2003) sea lice per fish were recorded.

Results

Distribution and origin

The proportion of survey sites with postsmolts was significantly higher in 2002, when both the outer Bay of Fundy and the upper Gulf of Maine were surveyed, than in 2001 or 2003, when either one or the other area was surveyed (Table 2; G test of independence, $P < 0.005$). Trawl deployment (i.e., mean tow time, tow speed, and trawl vertical opening) did not differ significantly between tows that captured salmon postsmolts and those that did not ($P > 0.05$, independent-samples t test). Environmental conditions (i.e., mean surface temperature and salinity) were also usually similar at all sites surveyed, but slight differences in water temperature in 2001 and in salinity in 2002 were recorded (independent-samples t test, $P < 0.05$). Capture rates at the sites where postsmolts were found decreased from an average of 6.7 postsmolts per tow in 2001 to 4.5 in 2002 and then to 1.8 in 2003. No schools of postsmolts were ever encountered at any trawling site; most often only a few postsmolts were captured at a site and the maximum numbers were 27 (2001), 25 (2002), and 7 (2003) postsmolts per tow.

No postsmolts were captured at any sites within the inner Bay of Fundy when the area was extensively surveyed in 2001, and captures within the outer Bay of Fundy were concentrated in two areas, in the main channel northeast of Grand Manan Island and just off the coast of Nova Scotia (Fig. 1). Postsmolts were captured in the same area east of Grand Manan when the outer Bay of Fundy was surveyed again in 2002 (Fig. 2*a*). Surveys in 2002 and 2003 showed that postsmolts were distributed more widely after leaving the Bay of Fundy as they fanned out into open waters of the

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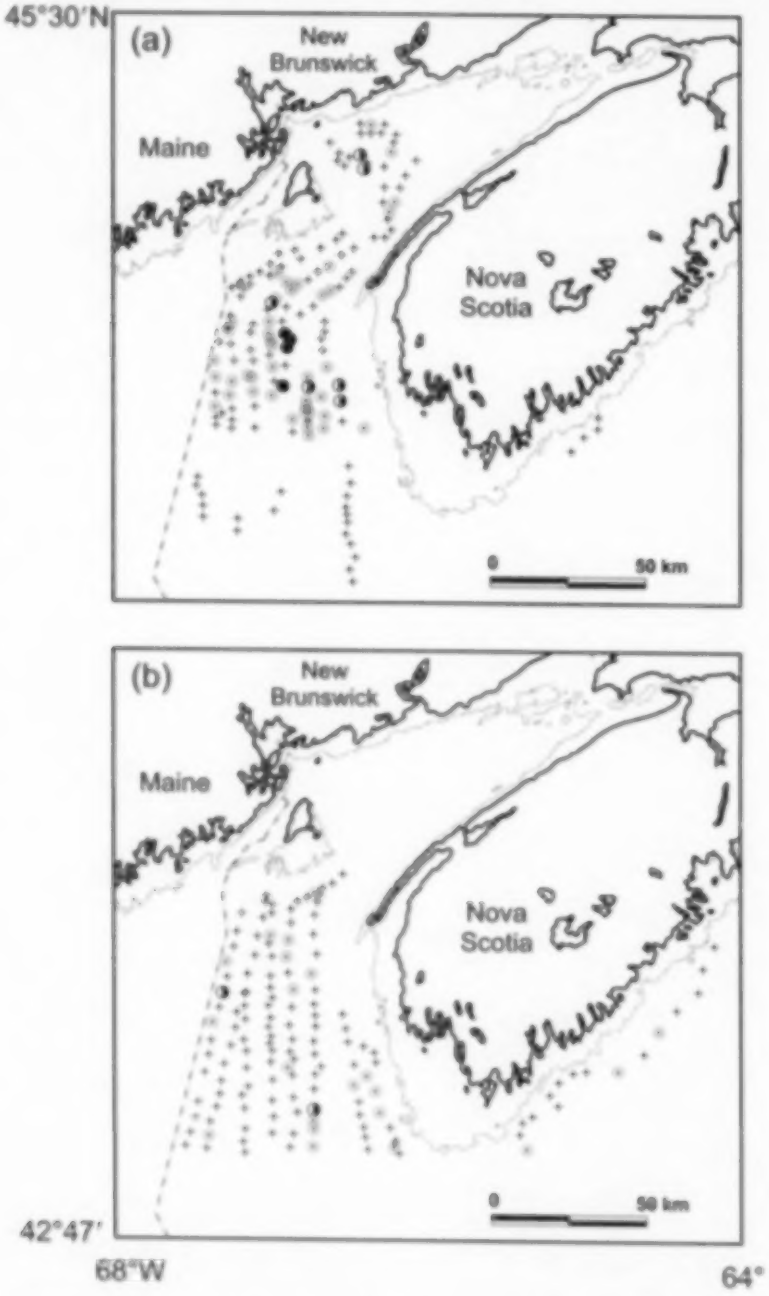
Fig. 2. Distribution and abundances (cross, 0 fish; solid circle within a circle, 1–5 fish; half-solid circle, 6–15 fish; solid circle, 16–30 fish) of Atlantic salmon postsmolts captured in the Bay of Fundy and Gulf of Maine. (*a*) The 2002 survey. (*b*) The 2003 survey. The 90-m isobath (·····) and International Maritime Boundary (— · — · —) are shown.



Gulf of Maine (Fig. 2). They tended to be more abundant off southwestern Nova Scotia than in the centre of the Gulf as they rounded the tip of Nova Scotia and headed toward the Atlantic Ocean. Postsmolts were also captured on the Scotian Shelf along southeastern Nova Scotia in 2003 (Fig. 2*b*).

Postsmolts were readily identified as being of either wild or hatchery origin with no overlap, and those of hatchery origin either were separated by country of origin based on unique identification tags or their origin was listed as unknown (Table 3). Lower proportions of postsmolts of wild origin were captured as the surveys moved from the Bay of Fundy in 2001 to progressively cover more of the Gulf of Maine in 2002 and 2003. Wild postsmolts belonged to two age groups; those of freshwater age 2 were dominant in

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Table 3. Numbers and size parameters (mean ± standard deviation) of Atlantic salmon postsmolts of different origins (wild or hatchery) captured during 2001–2003 surveys in the Bay of Fundy and Gulf of Maine.

		Hatchery			
	Wild	Canada	Maine	Unknown	Total
2001					
Number captured*	71 (56)	53 (42)	1 (<1)	2 (<2)	127
Fork length (cm)	17.2±1.91a	19.4±2.28b	20.8	17.1	
Weight (g)	52.8±19.5a	76.3±25.4b	90.3	63.8	
Condition factor	1.000±.085a	1.004±0.063a	1.003	1.033	
2002					
Number captured*	80 (35)	76 (33)	24 (11)	49 (21)	229
Fork length (cm)	17.6±1.44a	19.6±2.09b	20.5±1.19c	19.6±1.96b	
Weight (g)	55.3±14.4a	76.5±22.6b	85.8±14.2c	76.5±21.2b	
Condition factor	1.001±0.076a	0.979±0.060a	0.989±0.059a	0.988±0.066a	
2003					
Number captured*	10 (24)	16 (38)	6 (14)	10 (24)	42
Fork length (cm)	17.4±1.87a	18.0±2.08a	21.0±1.63b	17.9±2.40a	
Weight (g)	55.4±14.8a	62.3±22.1a	91.9±19.5b	61.8±25.0a	
Condition factor	1.037±0.053a	1.033±0.055a	0.984±0.054a	1.032±0.062a	

Note: Values within a row followed by a different letter are significantly different at $P \leq 0.05$ (independent-samples t test in 2001 and one-way analysis of variance followed by Duncan's multiple range test for 2002 and 2003).

*Numbers in parentheses are percentages.

2001 (89%) and 2002 (87%), but the proportion of those that were of age 3 increased almost 4 times in 2003 (40%). The proportions of hatchery-reared fish of Canadian origin remained relatively constant (33%–42%) over the 3 years, but there was a marked increase in the proportions that were of Maine origin (from 1% to 11%–14%) and of unknown origin (from 2% to 21%–24%) after 2001. All postsmolts of hatchery origin had been released as age-1 smolts; those of unknown origin had no marks or tags, but some had fin erosion and all had the freshwater circulus growth pattern typical of hatchery-reared fish (i.e., consistently wide and even spacing of circuli).

There were no obvious differences in the general distribution of postsmolts of wild and hatchery origin, in either the Bay of Fundy or the Gulf of Maine, over the 3 years (Fig. 3*a*). Fish of both origins were often captured together in the same tows. Wild and hatchery-reared postsmolts of known origin in Canada (i.e., those with river-specific marks) that were recaptured included fish from rivers both in the inner (Big Salmon River) and the outer (Saint John River system) Bay of Fundy (Fig. 3*b*). Postsmolts from the inner and outer bay and those of wild and hatchery origin were found in the same areas within the outer Bay of Fundy, out into Grand Manan Basin, and in the Gulf of Maine off southwest Nova Scotia. Recaptures of 31 hatchery-reared fish of known Maine origin were mostly concentrated across the Gulf of Maine off southwest Nova Scotia. All of these areas with postsmolts overlapped the reported location of catches of Atlantic herring by the commercial purse-seine fishery during May and June of 2001–2003 (Fig. 3*a*; M.J. Power, Department of Fisheries and Oceans, Science Branch, 531 Brandy Cove Road, St. Andrews, NB E5B 2L9, Canada, unpublished data).

The recapture rate of postsmolts with river-specific marks was higher for wild fish (0.09%) than for Canadian hatchery-reared fish (0.01%) over the 3 years. The recapture rate was highest for those wild postsmolts that originated from the inner Bay of Fundy (Big Salmon River, 0.32% in 2001 and 0.69% in 2002). None of the smolts marked in the St. Croix and Magaguadavic rivers located in Passamaquoddy Bay in the outer Bay of Fundy were ever recaptured as postsmolts.

Health and growth

The main difference in the external appearance of postsmolts of wild and hatchery origin was the presence of some fin erosion, usually dorsal, and minor scale loss (<5% of the body) on some hatchery-reared fish. Marked fin erosion was most common for postsmolts of unknown hatchery origin (57% occurrence in 2002 and 36% in 2003). Postsmolts that died during or soon after capture ($n = 13$ in 2001, $n = 44$ in 2002, and $n = 7$ in 2003) had extensive recent scale loss (up to 80% of the body) but no external lesions. This was thought to have been caused by the trawl net or in the attached tank when postsmolts were captured either with large numbers of other fish or with large fish. No bacterial or viral fish pathogens were identified by cell culture, and the reverse transcriptase polymerase chain reaction assay of kidney tissues was negative for the ISA virus for samples from the postsmolts that died; 17 wild postsmolts and 46 of hatchery origin were tested over 3 years.

The ectoparasitic copepod *Lepeophtheirus salmonis*, or salmon louse, was not found on any of the postsmolts. The sea louse *C. elongatus*, common on lumpfish, was found infrequently on postsmolts (2.4% in 2001, 4.4% in 2002, and 2.4% in 2003), and no more than one sea louse per fish was ever recorded either on wild postsmolts or hatchery-reared fish of Canadian and unknown origin. No lesions were present on postsmolts of either wild or hatchery origin that would have indicated that salmon lice had been present to any significant extent during the brief marine period.

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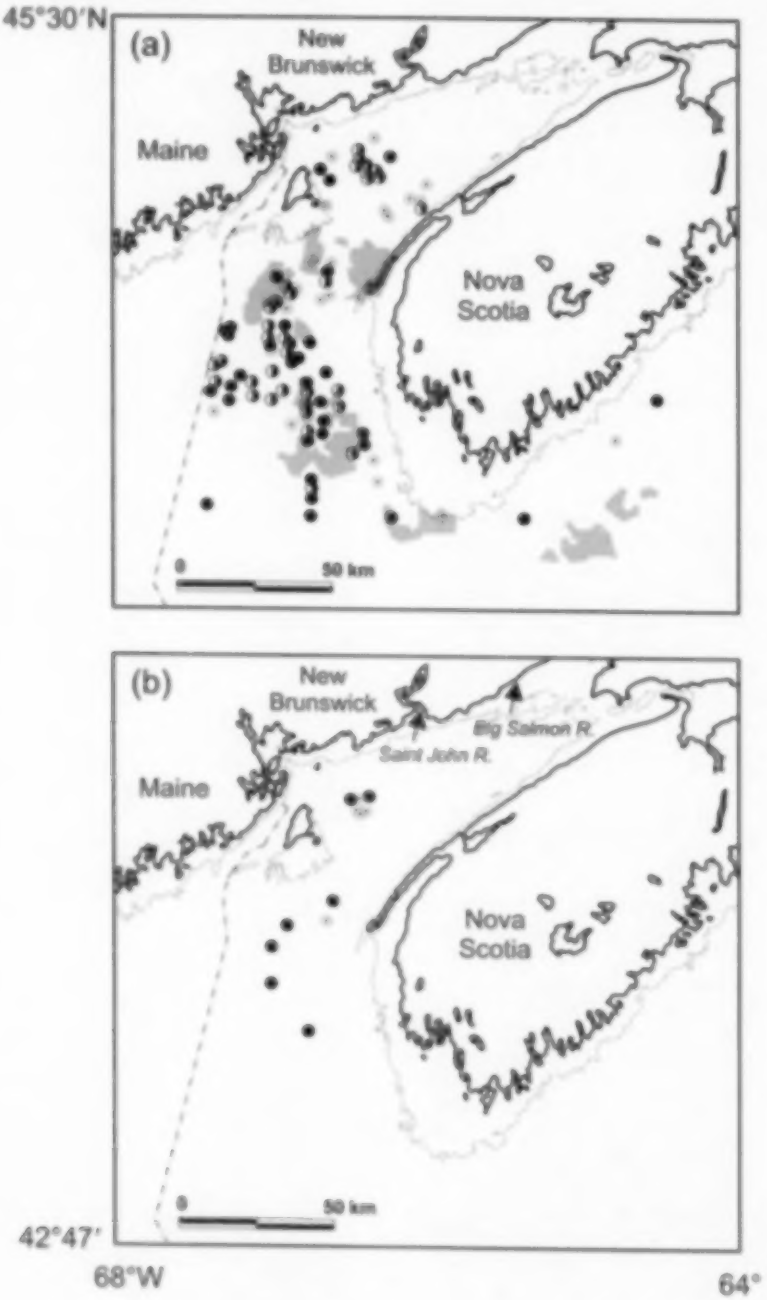
Fig. 3. Distribution of Atlantic salmon postsmolts of different origins in the Bay of Fundy and Gulf of Maine during 2001–2003. (*a*) Sites where wild (solid circle within a circle), hatchery-reared (solid circle), and both types of fish (half-solid circle) were captured. (*b*) Sites where fish from the Big Salmon River (solid circle) and Saint John River system (solid circle within a circle) were recaptured. The 90-m isobath (------) and International Maritime Boundary (— · — · —) are shown. In *a*, the areas of Atlantic herring (*Clupea harengus*) catches by the purse-seine fishery during May and June of 2001–2003 (shaded) are superimposed. In *b*, the mouths of the Big Salmon and Saint John rivers (arrows) are shown.



The mean length and weight of wild postsmolts were consistently similar (no significant differences, one-way analysis of variance among years, $P > 0.05$), and were significantly less than those of hatchery-reared fish regardless of their origin in all 3 years (Table 3; one-way analysis of variance, $P < 0.05$). Hatchery-reared fish of known Maine origin were

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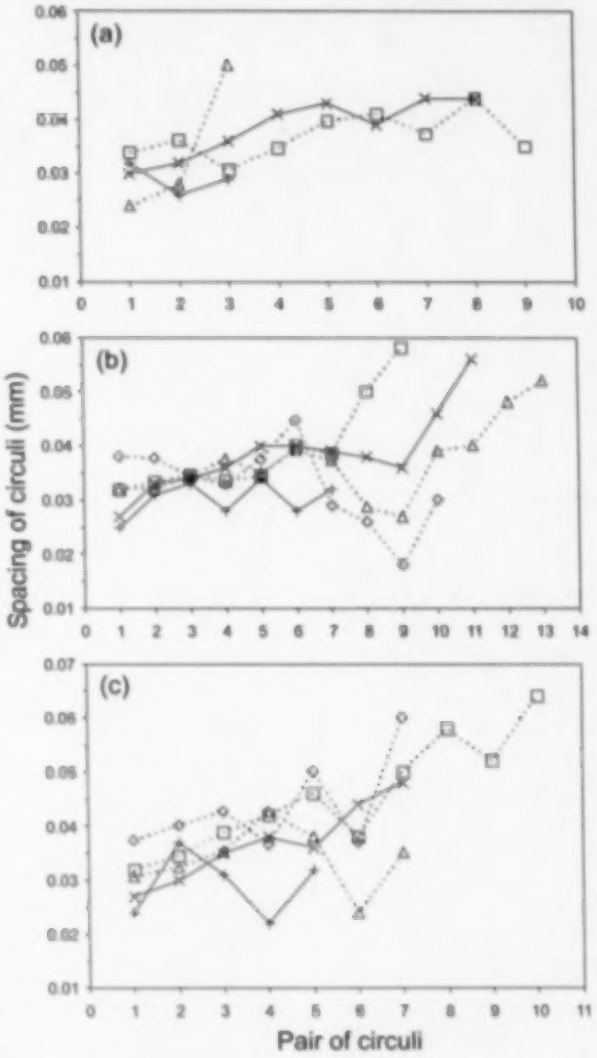
significantly larger than those of known Canadian origin, and those of unknown hatchery origin were similar to fish of known Canadian origin and significantly smaller than those of known Maine origin (one-way analysis of variance, $P < 0.05$). Mean condition factor was always close to unity, and it did not differ significantly among fish of different origin in all three years (one-way analysis of variance, $P < 0.05$).

Evidence of spring growth in the year of capture was provided by the presence of new circuli laid down on scales after the last winter annulus until capture, and by the spacing of these circuli (Fig. 4). This could have included growth that occurred in fresh water before smolts left the river (i.e., as seen in smolts from rivers with late migrants) and would have included any growth that took place after entry in the marine environment. Many postsmolts of hatchery origin did not show a winter annulus or a difference in spacing of circuli starting in the spring and they were excluded (Canada: 35% in 2001, 45% in 2002, and 12% in 2003; Maine: 70% in 2002 and 50% in 2003; unknown: 50% in 2001, 45% in 2002, and 9% in 2003).

Spacing of circuli for wild postsmolts that emigrated as age-2 smolts increased gradually with successive pairs of circuli, and spacing of circuli after the fourth pair was often significantly greater than the earlier spacing in all 3 years (one-way analysis of variance followed by Duncan's multiple range test, $P \leq 0.05$). In wild fish that emigrated as age-3 smolts, spacing did not show a similar increase, but they had 2–5 fewer circuli and had probably not been at sea as long as the age-2 group. Those postsmolts of hatchery origin that had a winter annulus also showed some increases in spacing of new circuli with successive pairs of circuli. Spacing of circuli was starting to increase more rapidly in postsmolts with the most circuli, but there was more variability in spacing after circulus pairs 5–6 as a result of the small sample size (i.e., few fish in each group had more than 6 circuli).

Fig. 4. Spacing of circuli on scales versus the pair of circuli representing spring growth in the year of capture for Atlantic salmon postsmolts of wild origin (solid line) that migrated as age-2 (×) and age-3 (+) smolts and for hatchery-reared fish (broken line) of Canadian (□), Maine (◇), and unknown (△) origin. (*a*) The 2001 survey. (*b*) The 2002 survey. (*c*) The 2003 survey.



Feeding habits

The stomachs of almost all postsmolts sampled (10 of 13 in 2001, all 43 in 2002, and all 7 in 2003) contained food items. More postsmolts fed on the crustaceans *Themisto* spp. (Amphipoda, Hyperiidae) and *Meganyctiphanes norvegica* and *Thysanoessa inermis* (Euphausiidae, or krill) than on any other prey items (Fig. 5). Fish (mostly larval and age-0) occurred in many stomachs, especially the sand lances (*Ammodytes* spp.) in 2001. Postsmolts consumed a greater variety of prey in 2002, when the survey covered both the Bay of Fundy and the Gulf of Maine, than in 2001 or 2003, when the surveys covered either one or the other area. The diet of postsmolts was the least diversified in 2003, when they were captured exclusively in the Gulf of Maine, where single species of amphipods and krill were mostly consumed. In contrast, several species of amphipods were consumed by postsmolts in 2001 and several species of krill were consumed in 2002. A wide variety of fish species were consumed in 2002, whereas in 2001 most identifiable fish in the diet were sand lances. Other food items were also more common in the diet of postsmolts in 2002 than in the other 2 years.

In addition to their occurrence in the largest number of postsmolt stomachs, amphipods (Hyperiidae) and then krill (Euphausiidae) were the most abundant prey items (Fig. 6*a*). Fish were less abundant as food items than the crustaceans, but the sand lances (Ammodytidae) and other fish were relatively abundant in 2001, when the survey was restricted to the Bay of Fundy. In 2002 and 2003, when the survey was extended to the Gulf of Maine, krill were more abundant prey items than in 2001 and the number of fish in the diet decreased.

Postsmolts of hatchery origin ($n = 46$) had considerably more food items in the stomach, especially amphipods (Hyperiidae) and krill (Euphausiidae), than did wild postsmolts ($n = 17$) (Fig. 6*b*). Amphipods were the most abundant items in the stomachs of postsmolts of hatchery or-

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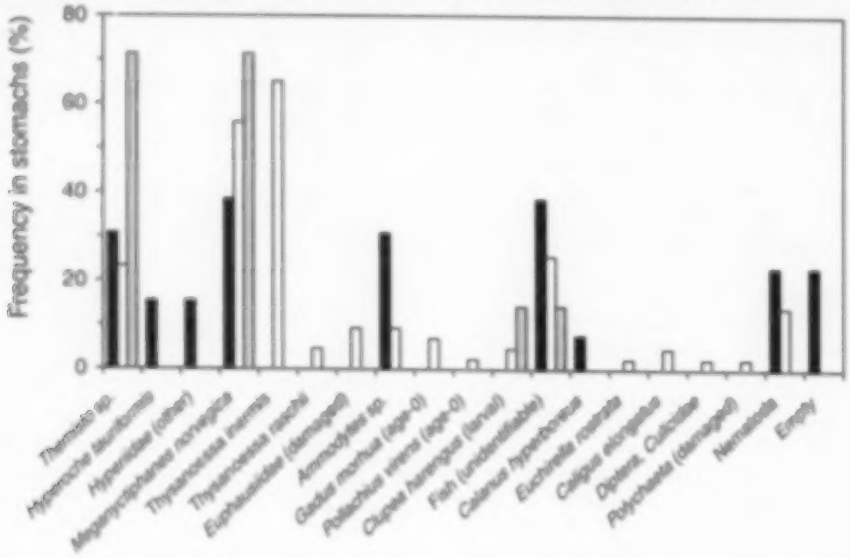
Fig. 5. Frequency of occurrence of food items in the stomachs of Atlantic salmon postsmolts in 2001 (solid bars), 2002 (open bars), and 2003 (shaded bars) expressed as the percentage of stomachs each year containing a specific prey item.



igin, whereas krill were the most abundant item in the stomachs of wild postsmolts. Fish, mostly sand lances, which were the largest prey item consumed, were almost twice as abundant in the diet of hatchery-reared fish as in that of wild postsmolts.

Discussion

The capture of live postsmolts in the Bay of Fundy and Gulf of Maine made it possible to evaluate the hypotheses that postsmolt migration was controlled by hydrography and that initial distribution was not influenced by origin (i.e., wild vs. hatchery and outer vs. inner Bay of Fundy stocks). It also made it possible to evaluate some of the more plausible hypotheses listed by Cairns (2001) concerning possible causes, during the early marine phase, for the decline in prefishery abundance of North American Atlantic salmon. These included disruption of migration and unfavourable habitat, intercepting commercial fisheries, absence of schooling for predator protection, infection by diseases or parasites endemic to Atlantic salmon farms, and failure to initiate the marine growth phase and find suitable and abundant prey.

It has been suggested that postsmolts are distributed according to prevailing surface currents either close to shore or in open waters in the northeast Atlantic Ocean, and that strong currents act as transportation vectors that facilitate migration (Jonsson et al. 1993; Holst et al. 2000). Hydrographic conditions and surface current transport vectors in the Bay of Fundy vary seasonally in a predictable manner. The capture of postsmolts near the surface placed them under the potential influence of surface currents. The largest concentration of postsmolts was within the Bay of Fundy at the head of the Grand Manan Basin, about 30 km east of the northern tip of Grand Manan Island. This is the area where the main currents leaving the Bay of Fundy tend to converge during spring (Chevrier and Trites 1960; Bumpus and Lauzier 1965). A secondary concentration of postsmolts within the bay close to the Nova Scotia shore could have been associated with the inflow of water to the bay from the Gulf of Maine, concentrated in a narrow band along the southeast shore of the Bay of Fundy (Bumpus and Lauzier 1965). Postsmolts could have ended up in this inflowing current because some water from the main outflow from the Bay of Fundy starts crossing to the Nova Scotia side at the level of Grand Manan Island, creating a counterclockwise gyre within the bay (Bumpus and Lauzier 1965). Postsmolts entrained in this current or gyre could then have been temporarily delayed in leaving the bay.

Postsmolts dispersed more widely along a southerly path that gradually curved eastward around southwest Nova Scotia, well outside the 90-m isobath as they entered the Gulf of Maine. The general outflow from the Bay of Fundy usually moves seaward over a broad area east of the 90-m isobath off Grand Manan Island (Bumpus and Lauzier 1965). The postsmolts were then possibly entrained into the Jordan Basin gyre, which has a strong easterly flowing segment during spring, when it reaches across to the Northeast Channel and out of the Gulf of Maine (Bumpus and Lauzier 1965). The possibility that some postsmolts were first entrained along the Maine Coastal Current, which flows in a southwesterly direction along the northern margin of the Gulf of Maine and feeds the easterly flowing arm of the Jordan Basin gyre in several locations (Chapman and Beardsley 1989; Beardsley et al. 1997), could not be ruled out because the surveys did not extend into US waters. This surface-transport vector could have accounted for the distribution of postsmolts of Maine origin along southwest Nova Scotia.

The hypothesis that differences in origin of smolts could affect the migration of postsmolts and their initial distribution in coastal areas was rejected. The similarity in distribution of postsmolts of wild and hatchery origin, regardless of

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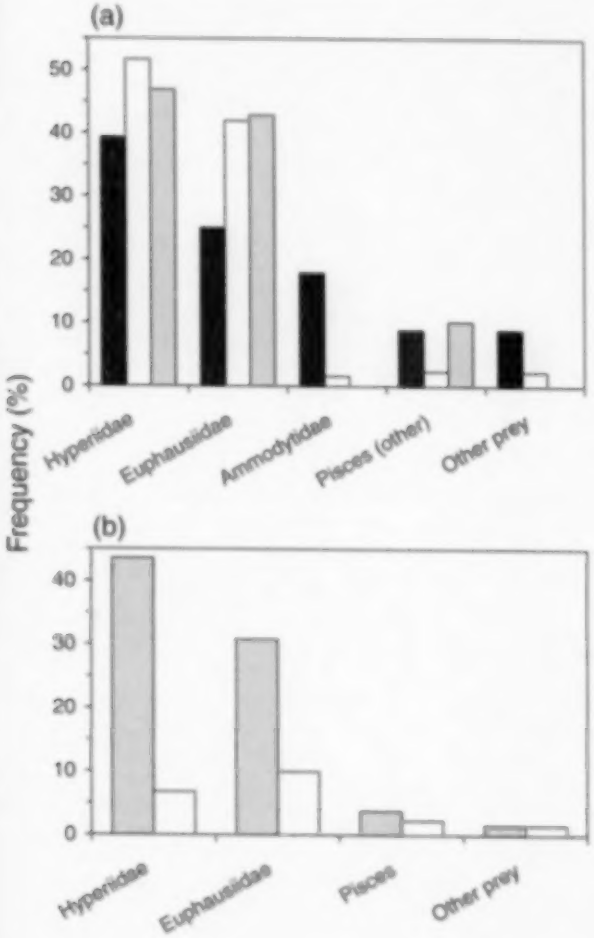

Fig. 6. Frequency of prey items belonging to major taxa in the stomachs of Atlantic salmon postsmolts expressed as the percentage of the total number of items in all stomachs. (*a*) All fish in 2001 (solid bars), 2002 (open bars), and 2003 (shaded bars). (*b*) Fish of hatchery origin (shaded bars) and wild origin (open bars) over 3 years.

the river or stock they came from, supported the importance of the link between postsmolt migration and general hydrography and surface current transport vectors in the Bay of Fundy. Verspoor et al. (2002) suggested that the genetic uniqueness of salmon stocks from some rivers located in the inner Bay of Fundy was possibly related to differences in marine migration and a failure of these postsmolts to leave the Bay of Fundy. This was partially based on the recapture of a few postsmolts in coastal fisheries within the Bay of Fundy during the summer (Jessop 1976). However, this was not supported by the recaptures of wild postsmolts from the Big Salmon River (i.e., an inner bay stock) in areas mostly outside the Bay of Fundy, well into the Gulf of Maine in the same areas and at the same time as postsmolts from rivers located in the outer Bay of Fundy or the northern Gulf of Maine. Postsmolts of inner Bay of Fundy origin followed the same migration route, at least initially in coastal waters, as those of outer-bay origin. A similar absence of stock-related differences in the migratory pattern of tagged postsmolts in Norwegian coastal waters was reported by Jonsson et al. (1993). This would ensure that postsmolts of different origins are exposed to the same navigational cues during a period when imprinting is thought to be important for future homing, and may help reduce straying from the general area of origin (Jonsson et al. 2003).

The origin of postsmolts changed as the survey moved from the Bay of Fundy (2001) to the Gulf of Maine (2002 and 2003). Salmon of wild origin made up a decreasing proportion of the population sampled in the Gulf of Maine, probably because of the large numbers of hatchery-reared smolts released in rivers of the Gulf of Maine (T.F. Sheehan, NOAA–Fisheries, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543, USA, personal communication). Postsmolts of unknown hatchery origin (i.e., unmarked but with scale features that confirmed hatchery origin) also increased to more than 20% of the population sampled in 2002 and 2003. A comparison of their size and new growth with that of known hatchery-reared fish indicated that some of these could have come from Maine hatcheries in 2002 and from Canadian hatcheries in 2003. No unmarked hatchery-reared fish were released in Canada in 2002, and almost none were without marks in Maine in 2003 (T.F. Sheehan, personal communication). The presence of a high proportion of marked fin erosion in this group compared with hatchery-reared fish of known origin indicated that some of the unmarked postsmolts could have recently escaped from Atlantic salmon farms in the Bay of Fundy, possibly during the spring transfer of smolts to net-pens.

The distribution and date of postsmolts catches indicated that they were successfully moving out of the Bay of Fundy and through the northern Gulf of Maine without apparent disruption of migration route or delay, regardless of their origin. Furthermore, environmental conditions in habitat where they were found were favourable to their survival and growth during spring. Postsmolts of all origins shared the same habitat and they were found to be in good condition when captured. The salinity (~31‰) was lower than that of full-strength seawater (salinity 33‰–35‰), which could have reduced the initial physiological challenge and provided a period of seawater adaptation as postsmolts made the transition to marine conditions (Stefansson et al. 2003). However, successful adaptation to full-strength seawater should be verified with physiological measurements and seawater challenge. The low water temperature (~6–9 °C) throughout the survey area at the time of migration was within the surface-temperature range where Atlantic salmon are commonly caught at sea (Reddin and Friedland 1993; Holm et al. 2000). The temperature was considered suitable for relatively rapid marine growth, based on observations from Atlantic salmon farms in the outer Bay of Fundy.

The hypothesis that intercepting commercial fisheries in coastal areas of the Bay of Fundy and Gulf of Maine could significantly affect postsmolt survival was neither accepted nor rejected. In coastal areas where postsmolts migrate near shore, they have been intercepted by weirs for Atlantic herring (Jessop 1976; Lacroix et al. 2004). The weir fishery was

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extensive in the Bay of Fundy but its impact on salmon stocks could not be evaluated because no significant by-catches have been reported. There was a significant commercial purse-seine fishery for Atlantic herring during May and June each survey year that considerably overlapped the distribution of salmon postsmolts as they left the Bay of Fundy and entered the Gulf of Maine. This spatial and temporal overlap in habitat indicated that postsmolts migrating near the surface could have been intercepted and captured in purse seines, but no by-catches have been reported. The two species were found to occur together (e.g., 80% of tows with postsmolts also captured herring in the 2002 survey), and postsmolts were targeted regardless of their origin. Holm et al. (2003) indicated that in the northeast Atlantic Ocean, there could be a significant by-catch of salmon postsmolts by the extensive surface trawl fishery for mackerel that takes place in the international zone in the Norwegian Sea because of similar spatial and temporal overlap. In contrast, few pelagic trawlers were involved in the herring fishery in the Bay of Fundy or on the Canadian side of the International Maritime Boundary in the Gulf of Maine. Nevertheless, the potential for the various commercial fisheries to intercept salmon stocks in the Bay of Fundy should be examined more closely, and this should be extended to the US portion of the Gulf of Maine, where the fishery differs (i.e., pelagic trawlers predominate) and may have a greater potential impact.

Lacroix et al. (2004) indicated that postsmolt losses to predators could be greater in areas where they migrate near Atlantic salmon farms. Although the importance of postsmolt losses to predators could not be addressed by the surveys, the consistently low catches of wild postsmolts indicated that they were probably too scarce throughout the areas surveyed to form the large schools that can act as predator defence and reduce predation risk for pelagic fishes (Pitcher and Parrish 1993). Postsmolts have a natural schooling tendency, at least to some degree, during daytime (Dutil and Coutu 1988; Skilbrei et al. 1994). The very low abundance of postsmolts could create a downward spiralling effect by increasing the probability of predation. Catches did reveal a positive association of some species, such as the spiny dogfish, with salmon postsmolts (i.e., they were caught infrequently but almost always with salmon) that could be indicative of predation.

The survey found no evidence to support the hypothesis that parasites or diseases found in salmon farms or hatcheries were affecting postsmolts leaving the Bay of Fundy. Salmon lice (*L. salmonis*) and the ISA virus often occur in epidemic proportions in Atlantic salmon farms in the Bay of Fundy (B.D. Chang, Department of Fisheries and Oceans, Science Branch, 531 Brandy Cove Road, St. Andrews, NB E5B 2L9, Canada, unpublished data). Most salmon farms are located in the Quoddy Region (Passamaquoddy and Cobscook bays and adjacent areas) and along the eastern and southern shores of Grand Manan Island. Salmon from rivers in the Quoddy Region migrate through these areas of very high farm density (Lacroix et al. 2004). The excellent health of postsmolts captured in the Bay of Fundy and Gulf of Maine (e.g., no salmon lice, lesions or other pathologies, or bacterial or viral pathogens) indicated that their survival over the long term was probably not compromised by the diseases or parasites associated with salmon farms along their migration route. Had migrating postsmolts been infected by these diseases or parasites, they would have been alive but obviously infected at the time of the surveys. Mortality due to salmon lice usually appears more than 3 weeks after salmon are infected, by which time they show visible symptoms of advanced impact, such as mechanical damage consisting of severe skin erosion and lesions, especially on the head and operculum (Grimnes and Jakobsen 1996).

Salmon need to start feeding on marine prey and to increase their growth rate soon after they enter marine habitat to survive a long oceanic migration. Atlantic salmon smolts are generally considered to be "energy-deficient" and have low energy reserves for somatic growth upon leaving the river and during the early marine phase (Jonsson and Jonsson 2003; Stefansson et al. 2003). Early marine growth of Atlantic salmon has been strongly linked to ocean climate and overall marine survival (Friedland et al. 2000), and a rapid increase in size could also decrease the probability of predation at sea if small postsmolts were easier prey than large ones as suggested by Hansen et al. (2003). There was no evidence that the growth of the majority of postsmolts of either wild or hatchery origin was negatively impacted in coastal habitat. The presence of new spring circuli (i.e., as defined by Friedland et al. 1996) on scales of postsmolts in the Bay of Fundy and Gulf of Maine and the increasing spacing of circuli were indicative of an increasing rate of marine growth in the period just before capture. This is supported by the large increase in weight of wild postsmolts in a short time span over that of wild smolts marked in several rivers (G.L. Lacroix, unpublished data). Holst et al. (2000) reached a similar conclusion, that marine growth opportunities were initially not critical, based on the size of postsmolts in the northeast Atlantic Ocean.

The hypothesis that poor initial growth affected postsmolt survival in the early weeks at sea was rejected, but with the following cautions. Although marine growth was apparently increasing, the spring spacing of circuli indicated that it may not have been as rapid as expected when compared with spacing of circuli for postsmolts from nearby or more southerly rivers (i.e., Connecticut and Penobscot rivers; Friedland et al. 1996) for the same period. Instead, spacing of circuli was comparable to that of postsmolts caught in the Labrador Sea (Friedland and Reddin 2000), probably because of the consistently cold water in the Bay of Fundy compared with adjacent areas (Beardsley et al. 1997). This slower growth of northern or cold-water stocks could eventually have some implications for survival if rapid growth during the critical early period of marine residency conferred a survival advantage as hypothesized by Friedland et al. (2000). Similarly, the greater spacing of circuli observed for wild postsmolts of age 2 than for those of age 3 during the early period in the Bay of Fundy could have similar implications for their relative survival.

Salmon are considered to be pelagic and midwater predators at sea, supporting a rapid growth rate by exploiting a wide range of invertebrates and fish prey at the upper end of the available size spectrum (e.g., Jacobsen and Hansen 2000). Therefore, postsmolts must change their diet from terrestrial or freshwater insects near shore to pelagic items with a high lipid content, such as larval fish and crustacean

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amphipods as they migrate farther offshore. Such a shift in prey has generally been observed for postsmolts as they progress from estuary to middle and outer zones of Norwegian fjords (Rikardsen et al. 2004). However, failure to either target new prey or locate abundant prey, as observed by Rikardsen et al. (2004) in some fjord systems, could influence postsmolt growth and survival. There was no evidence that food supply was limiting to postsmolts of wild or hatchery origin as they migrated from coastal habitat in the Bay of Fundy to more open marine habitat in the Gulf of Maine. They fed opportunistically on a small number of pelagic prey species that changed along the migration route. Sand lance and fish larvae were frequent prey while postsmolts were in the Bay of Fundy (2001), but were infrequent in the diet as postsmolts moved into the Gulf of Maine (2002, 2003), where they were replaced by crustaceans (amphipods and krill). Such differences in postsmolt feeding would probably be due to spatial and temporal differences in prey availability as observed by Rikardsen et al. (2004) within and between different types of fjord systems. Prey size did not seem to limit the diet of the smaller wild postsmolts compared with hatchery-reared fish. Sand lance, the largest prey item, was an important component of the diet of wild postsmolts while they were in the Bay of Fundy. Krill that were more than 10 times larger than amphipods were the most important food item of wild postsmolts, especially when they moved out of the bay. However, the large hatchery-reared fish consumed a much greater quantity of food items than did wild postsmolts (6 times more amphipods and 3 times more krill), which could have conferred a size-related competitive advantage, resulting in higher marine survival.

The near absence of terrestrial insects and freshwater invertebrates, which occur in quite large numbers in the neuston of the Bay of Fundy (Locke and Corey 1986), in the diet of postsmolts indicated that they had made the transition from a habit of feeding on surface drift to one of pelagic foraging by the time they reached the outer Bay of Fundy. Similarly, we found few of the amphipod and none of the isopod species reported by Locke and Corey (1989) in the neuston of the Bay of Fundy and adjacent waters in the diet of postsmolts. Most of those species tend to be associated with drifting littoral vegetation at the surface. However, the euphausiids *M. norvegica* and *T. inermis*, both of which were important food items for postsmolts, are ubiquitous in the neuston of the Bay of Fundy from spring to autumn, their dispersal being influenced by major currents (Locke and Corey 1988).

The rate of recapture of marked smolts was low and varied considerably among postsmolts of different origins, but any attempt to interpret these differences as differences in survival would be speculative because of the limited scope of the marking and surveys and regional differences in the dates of smolt emigration or release. The highest recapture rate was for wild postsmolts that originated from the Big Salmon River in the inner Bay of Fundy, indicating that they were successful in leaving the bay after a few weeks at sea. This is significant because the salmon stock from that river has been listed as endangered (Amiro 2003). High marine mortality is assumed to be a main contributing factor, but the survey indicated that early marine survival of postsmolts from the inner bay might be as good as or better than that of outer-bay stocks. The absence of recaptures of wild salmon originating from Passamaquoddy Bay indicated that some factors associated with the high density of Atlantic salmon farms within that bay and all along the narrow route that postsmolts must travel to reach the Bay of Fundy could be reducing their survival (e.g., because of an increase in predators; Lacroix et al. 2004). However, few smolts from that area were marked, thereby reducing the expectation of postsmolt recaptures.

Overall, no single overriding factor was identified that could account for the extensive decline in abundance of Atlantic salmon that originated from most rivers around the Bay of Fundy. Nevertheless, too few wild postsmolts were leaving the Bay of Fundy to expect any significant returns of wild adult salmon to the region. Postsmolt catches reflected the very low abundance of wild salmon in the Bay of Fundy and Gulf of Maine and the increasing importance of and reliance on salmon of hatchery origin for maintaining stocks. More attention should therefore be paid to the performance of hatchery-reared salmon at sea relative to that of wild salmon, to assess the potential impact on wild stocks of this shift in the overall population to fish of hatchery origin. This assessment should include hatchery-reared salmon that escape from marine farms. The rejection of some of the hypotheses formulated to explain the extensive losses of salmon at sea, at least for postsmolts in coastal habitat, is significant because it provides a rationale for focusing on other potential factors. Factors such as commercial pelagic fisheries in the Gulf of Maine and the importance and potential impact of various predators are considered to merit further attention. A shift in focus to those factors that could affect salmon farther off at sea is probably also warranted.

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Estimating catch-at-age by combining data from different sources

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Abstract: Estimating the catch-at-age of commercial fish species is an important part of the quota-setting process for many different species and almost all countries with a fishing fleet. Current procedures are usually very time-consuming and somewhat ad hoc, and the estimates have no measure of uncertainty. We previously developed a method for catch-at-age of Norwegian Atlantic cod (*Gadus morhua*), but this only considered aged fish sampled randomly from random hauls. In most countries, the sampling scheme is not so simple. There are usually a very large number of length-only samples from which the age must be estimated using an age–length relationship, and often some or all of the age samples are collected from data that are first stratified by length. This adds considerably to the difficulties in the estimation. In this paper, we model the three different kinds of data simultaneously using a development of our earlier Bayesian hierarchical model. This enables us to obtain estimates of the catch-at-age with appropriate uncertainty and also to provide advice on how best to sample data in the future. The data types are random samples of age, length, and weight; age and weight stratified by length; and length only.

Résumé : L'estimation de la récolte en fonction de l'âge est une étape importante du processus de définition des quotas pour plusieurs espèces et dans presque tous les pays qui possèdent une flotte de pêche. Les méthodes courantes exigent beaucoup de temps et elles sont ajustées à des situations particulières et elles ne comportent pas de mesure d'incertitude. Nous avons développé antérieurement une méthode pour estimer la capture en fonction de l'âge chez la morue franche (*Gadus morhua*) de Norvège, mais elle ne tient compte que des poissons d'âge connu échantillonnés au hasard dans des récoltes aléatoires. Dans la plupart des pays, le plan d'échantillonnage est loin d'être aussi simple. Il y a généralement un très grand nombre d'échantillons comportant seulement des longueurs, dont on doit estimer l'âge à l'aide d'une relation âge–longueur, et souvent quelques-uns ou même tous les échantillons contenant des déterminations d'âge ont été tirés de données préalablement stratifiées d'après la longueur. Une modification de notre modèle hiérarchique bayésien antérieur nous permet de traiter les trois types de données simultanément. Nous obtenons ainsi des estimations de la capture en fonction de l'âge assorties d'une mesure d'incertitude appropriée; nous proposons aussi comment mieux échantillonner les données dans le futur. Les types de données utilisées sont des échantillons aléatoires des âges, des longueurs et des masses; des âges et des masses stratifiées en fonction de la longueur; et des longueurs seules.

[Traduit par la Rédaction]

Introduction

As part of the process of setting fishing quotas, every country in Europe with a fishing fleet reports the total annual catch-at-age of various species to the International Council for the Exploration of the Seas. Strictly speaking, catch-at-age means the total number of fish caught at each age. However, it is common to group less frequent ages together to form a number of age groups. In our case, fish older than 12 years are considered one group. Also, an unknown number of fish are caught but discarded at sea. We do not take into account these discards. This kind of data is sometimes known as market sampling, although in Norway, a substantial part of the data is taken directly from the boat rather than from the market.

The weight of the total catch is usually considered to be known at a fairly fine resolution (in Norway, season by gear by area by year) and the aim of the analysis is (*i*) to estimate proportion-at-age and (*ii*) to estimate the mean weight of fish to convert the total to numbers from weight. A variety of different sampling schemes have been established for this purpose, and the data are analysed in a range of different ways. A common feature of most of these methods is that there is no statistical model for the sampling process. Ad

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hoc methods are used, which are very time-consuming and rely on individual judgement, which by definition is not repeatable. The Norwegian approach is outlined in Hirst et al. (2004). With such methods, it is very difficult to get a measure of the uncertainty in the reported results. To address this problem, Hirst et al. (2004) developed a Bayesian hierarchical model for the Norwegian catch of northeast Atlantic cod (*Gadus morhua*). This model, however, only addressed the strategy of sampling fish at random from random boats and estimating the age and measuring the weight of all of the fish in the sample. There was no modelling of length in this paper, and weight was modelled directly in terms of age.

The Norwegian sampling scheme is probably unique in Europe. Elsewhere, there is an emphasis on sampling large numbers of fish for which only length is measured and weighing and estimating the ages of only a few of these. These aged fish are usually stratified by length (e.g., one fish from each 5-cm length-class in a sample might be aged). This kind of sampling in fact takes place to a lesser degree in Norway as well, and additional length-only or age-given-length data (often from independent sources such as the Coast Guard) are utilized in the estimation. In this paper, we develop a common model for all of these kinds of data.

The difficulties in the analysis arise mostly because it is not possible to develop a proper sampling scheme for fishing vessels. In general, they are sampled when and if they are available. There are important differences in the catch between different seasons, fishing gears, and regions of the sea, and if we call each combination of these factors a cell, there are necessarily many cells with no samples. In addition, there is a large within-haul correlation in the ages and sizes of the caught fish. Thus, the effective sample size is very much smaller than the number of fish sampled (see Aanes and Pennington 2003). This leads to a larger uncertainty than would be apparent from a naive assumption of independence of fish.

The aim of this paper is to establish a proper statistical framework within which market sampling data can be analysed. The hierarchical framework is very appropriate for this kind of modelling because it can easily accommodate the different sampling schemes and because it provides a full measure of uncertainty. Random effects are included into the model to take into account correlation between samples from the same haul.

Bayesian approaches are usually used for making inference in hierarchical models (Gelman et al. 1995) and are now slowly emerging into the fisheries community (e.g., see Millar and Meyer 2000 and references therein). They have also been used in stock assessments (Hilborn and Lierman 1998; Lewy and Nielsen 2003), estimation of depensation (Lierman and Hilborn 1997), and estimation of biological reference points (Prevost et al. 2003).

Materials and methods

Data

There are three main sources of data available to the Norwegian Institute of Marine Research (IMR), which is responsible for estimating the catch-at-age of cod in Norway.

(*i*) The *Amigo* is a research vessel hired by IMR that sails from port to port along the north Norwegian coast over a period of about 6 weeks four times a year (roughly corresponding to the four seasons). At each port, it takes a sample of about 80 fish from any boats available at the time. The fish sampled from a boat are intended to be a sample from a single haul, and this is usually achieved. In some cases, there may have been some mixing of hauls before the samples are taken, however. There is rarely more than one boat available. The fish are weighed, the length measured, and the otoliths extracted for estimating the age of the fish (Campana 2001). Each year, about 200 boats, and thus about 16 000 fish, are sampled. Note that the program only samples landings. There are an unknown number of small fish discarded at sea, although we refer to catch-at-age in this paper.

(*ii*) The Coast Guard, whose tasks include making sure that the Norwegian fishery laws and regulations are kept, have the right to inspect any vessel and to sample the catch. In most cases, the vessels sampled by the Coast Guard are a random sample of the vessels operating within an area, but in a few cases, the inspections may be based on suspicion of illegal fishing. Thus, it might be expected that some of the samples would be biased or unrepresentative for the total catch, although this does not appear to be the case. In general, these samples will only provide length measurements of the fish sampled, although occasionally, there are some ages and weights as well. The Coast Guard samples more of the trawlers than the *Amigo*. The number of fish sampled in each haul is very variable but averages about 100.

(*iii*) The reference fleet is a fleet of commercial fishing vessels that have agreed to provide IMR with data on their catch. The reference fleet was started in 2001 with six vessels and consists currently of eight vessels. The fleet targets several commercially important species including cod. This sampling program is developing and will expand in the years ahead. So far, it has consisted mostly of length-only data, but there are an increasing number of age samples. In 2002, this fleet sampled approximately 500 hauls of cod with around 90 fish sampled in each haul.

The "cells" that we consider in this paper are the individual combinations of the regions in Fig. 1, season (corresponding roughly to the quarters of the year), gear (bottom trawl, Danish seine, gill net, longline, and handline), and year (1995–2002, but the reference fleet only began in 2001). One cell therefore represents one gear in one region in one season of one year. Our sampling unit is the haul. The Coast Guard and reference fleet always provide data from individual hauls, and although we suspect that the *Amigo* data sometimes contain fish from mixed hauls (although always from the same cell), we do not believe that this is an important effect. We do not consider the actual boat that was sampled to be of interest. For the *Amigo* and Coast Guard data, it is very unlikely that the same boat would be sampled twice (at least in the same year), but clearly, the reference fleet provides many samples from the same few boats. Any boat effect, however, is largely due to the particular gear being used, and the remaining effect will be very small compared with the differences between hauls.

For the purposes of the analyses in this paper, we have formed super-regions by grouping the regions in the map. In

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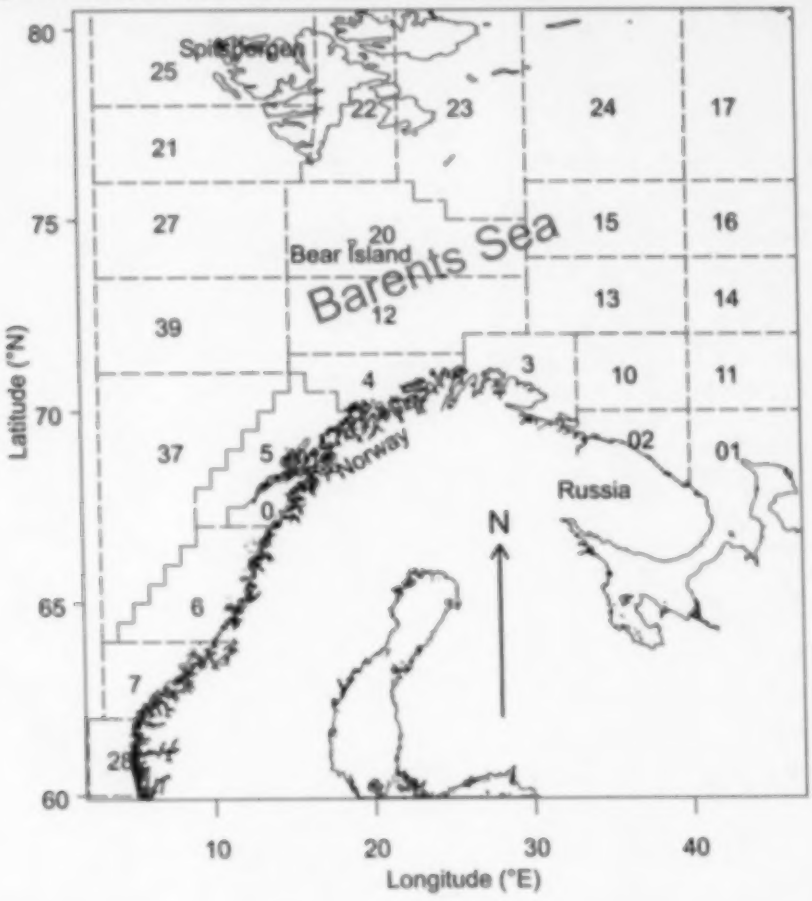
Fig. 1. Map of sampling area showing the Norwegian Directorate of Fisheries statistical regions in which the total catch is reported.



fact, we have used the eight standard IMR groups of (3, 2, 10, 11, 13, 14, 15, 16, 17, 24, 1), (12), (4), (5, 37, 39), (0), (6), (7, 28), and (20, 21, 22, 23, 25, 27). It is necessary to do some grouping because most regions have little or no data, although other groupings are possible. We have grouped ages over 12 together, and there are no fish younger than 2, giving us 12 age groups.

In the next sections, we develop the various components of the model: the proportion-at-age, length-given-age, and weight-given-length. The components are brought together in the likelihood for the whole data set. We then explain how to obtain samples from the posterior distribution of the parameters given the data using Markov Chain Monte Carlo (MCMC) (Gilks et al. 1996). Finally, we show some results and illustrate how these change when different data sources are included in the analysis. This also enables us to provide some guidance on how best to sample in the future.

Model for proportion-at-age

The samples from a boat are assumed to be randomly drawn from the total population of fish in that haul, and the hauls are themselves assumed to be randomly sampled from all of those within the appropriate cell. The numbers-at-age in a sample from haul h from cell c, $\mathbf{X}_{c,h}$, are therefore multinomial:

$$\mathbf{X}_{c,h} \sim \text{multinomial}(\boldsymbol{p}_{c,h}, n_{c,h})$$

The number of fish sampled from the haul, $n_{c,h}$, is assumed not to depend in any way on $\boldsymbol{p}_{c,h}$.

The vector of proportions-at-age in the haul, $\boldsymbol{p}_{c,h}$, has A elements, one for each age group. Let $p_{c,h}(a)$ be the ath element, where $0 \le p_{c,h}(a) \le 1$ and $\sum_{a'=1}^{A} p_{c,h}(a') = 1$. This is reparameterized as

$$p_{c,h}(a) = \frac{\exp(\alpha^{a}_{c,h})}{\sum_{a'=1}^{A} \exp(\alpha^{a'}_{c,h})}$$

We model $\alpha^{a}_{c,h}$ in terms of the various covariates as

$$\alpha^{a}_{c,h} = \alpha^{\text{base},a} + \alpha^{\text{year},a}_{\text{yr}(c)} + \alpha^{\text{season},a}_{\text{ss}(c)} + \alpha^{\text{gear},a}_{\text{g}(c)} + \zeta^{\text{region},a}_{\text{gr}(c)} + \zeta^{\text{cell},a}_{c} + \zeta^{\text{haul},a}_{c,h}$$

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Here, $y(c)$ means the year, $s(c)$ the season, $g(c)$ the gear, and $r(c)$ the region corresponding to cell c. From now on for clarity, we drop the c and just refer to $\alpha_y^{year,\alpha}$, etc.

The α terms and $\zeta_r^{region,\alpha}$ are the main effects for year, season, gear, and region. The α terms are fixed effects and $\zeta_r^{region,\alpha}$ is a spatially smoothed random effect. It is necessary to estimate the proportions in areas with no data, and our approach is to introduce some spatial smoothing. This is accomplished by assuming that $\zeta_r^{region,\alpha}$ follows a Gaussian conditional autoregressive distribution (e.g., Carlin and Louis 1996). The alternative would be to group areas such that there were none with no data. This is unsatisfactory for several reasons, particularly because the grouping would have to be done differently in each analysis. It is assumed that there will always be some data for all levels of the fixed effects that are of interest. The $\zeta_c^{cell,\alpha}$ terms are independent random effects modelling the interactions between the main effects (e.g., see Gelman et al. 1995). In other words, the differences between the fit from the main-effects-only model and the true cell means are modelled by the $\zeta_c^{cell,\alpha}$ terms. The differences between hauls within a cell are modelled by the random effects $\zeta_{c,h}^{haul,\alpha}$. These must be random (rather than fixed) effects because there are many cells and hauls with no data. We assume that all of the interactions (i.e., the $\zeta_c^{cell,\alpha}$ terms) can be modelled by a single distribution. It would be plausible to assume that some interactions (e.g., between season and year) had a higher variance than others, but we have found no evidence for this in the data (for more details of the parameters, including identifiability constraints and the prior distributions, see Appendix A).

Models for length-given-age and weight-given-length

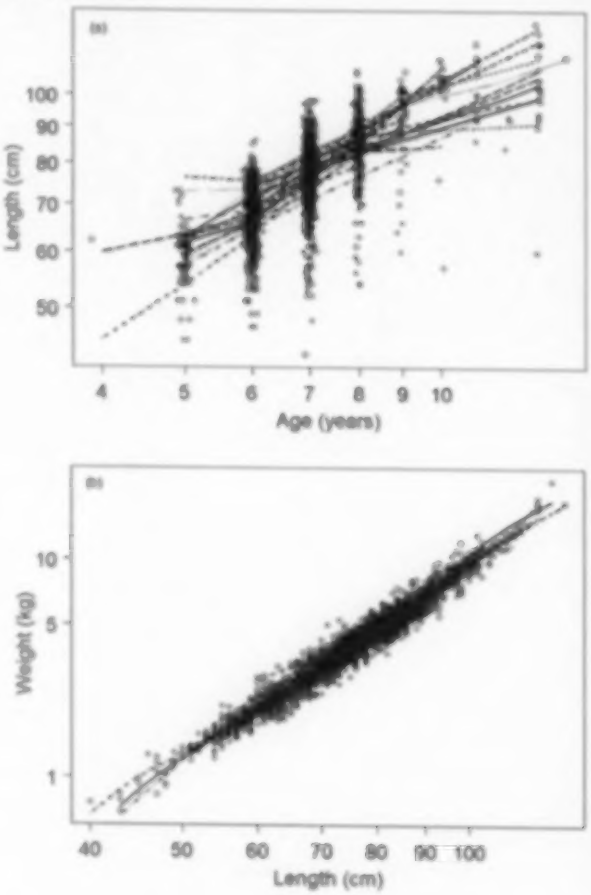
We plot log(length) against log(age) for all of the hauls in one cell (Fig. 2*a*). The lines are nonparametric fits for the individual hauls using the Splus function "supsmu". The equivalent plot of log(weight) against log(length) is also provided (Fig. 2*b*). It can be seen that there is a reasonably linear relationship between the variables, with some differences between hauls. We model both relationships as linear with a constant slope and variable intercept. This is unproblematic for the length–weight relationship, but the age–length model could be improved. There is some evidence of a nonlinear relationship, which may cause problems at high and low ages. Other models would be possible and may in particular be necessary for other species with different growth patterns. The von Bertalanffy (1938) growth curve is commonly used in fisheries science and could be used as an alternative. See Haddon (2001) for a discussion of possible growth curves.

Note that it would be possible to model weight given age directly but that modelling it via length enables us to get a better estimate of the mean weight-at-age in cells with length but no age data. Since the length–weight relationship is so strong, there would in any case be no advantage in modelling weight directly in terms of age.

We assume that length-given-age and weight-given-length are log-normal, with constant variances, and means linear in log(age) and log(length), respectively, in an individual haul. The slopes are constant, but the intercepts vary between cells and boats within a cell:

$$\log(\text{length}_{c,h,f}) = \beta_{0,c,h} + \beta_1 \log(\text{age}_{c,h,f}) + \varepsilon_{c,h,f}^{fish}$$

Fig. 2. Plots showing the relationship between (*a*) length and age and (*b*) weight and length for all hauls within a cell. The lines are nonparametric fits for individual hauls. Ages have been jittered for clarity.



$$\log(\text{weight}_{c,h,f}) = \delta_{0,c,h} + \delta_1 \log(\text{length}_{c,h,f}) + v_{c,h,f}^{fish}$$

Here, $\text{length}_{c,h,f}$ is the length of the fth fish from haul h in cell c, $\text{weight}_{c,h,f}$ its weight, and $\text{age}_{c,h,f}$ its age; $\varepsilon_{c,h,f}^{fish}$ and $v_{c,h,f}^{fish}$ are independent zero mean Gaussian random variables.

The slopes β_1 and δ_1 are common to all cells and hauls, and the intercepts $\beta_{0,c,h}$ and $\delta_{0,c,h}$ are given by

$$\beta_{0,c,h} = \beta^{base} + \beta_y^{year} + \beta_s^{season} + \beta_g^{gear} + \varepsilon_r^{region} + \varepsilon_c^{cell} + \varepsilon_{c,h}^{haul}$$

$$\delta_{0,c,h} = \delta^{base} + \delta_y^{year} + \delta_s^{season} + \delta_g^{gear} + v_r^{region} + v_c^{cell} + v_{c,h}^{haul}$$

ε_r^{region} and v_r^{region} are conditional autoregressive distribution parameters with properties to those of $\zeta_r^{region,\alpha}$ in the age model (see Appendix A). ε_c^{cell} and v_c^{cell} and are random "all interactions" effects equivalent to $\zeta_c^{cell,\alpha}$. ε_c^{haul} and v_c^{haul} are between-haul random terms. The β and δ terms are fixed effects similar to the α terms in the model for proportions-at-age (for more details, see Appendix A).

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Inference on unknown parameters

Parts of the model are standard, and ordinary methods such as maximum likelihood could have been applied. This is certainly true for the length-given-age model and the weight-given-length model. With all ages known and with no random effects involved in the age model also, the parameters in the multinomial model describing the age proportions could easily be found by maximum likelihood. Both the inclusion of random effects in the multinomial model and missing ages make maximum likelihood estimation much more complicated. Further, a frequentist approach to estimation makes it difficult to take the uncertainty in the parameters into account. It is probably possible to use a frequentist model, perhaps by using the Expectation Maximization (EM) algorithm to maximize the likelihood in the presence of missing data, combined with a parametric bootstrap to obtain the uncertainty. This does not seem to us to be the best approach to the problem, however.

Our approach has been the Bayesian one. The full information about the parameters (including random effects) is described through the posterior distribution. This distribution is difficult to calculate, but approximations can be obtained through Monte Carlo sampling. The actual sampling is performed through an MCMC algorithm using a combination of Gibbs sampling and Metropolis–Hastings steps. The details are given in Appendix B, but in outline, the approach is as follows. (*i*) If the ages and lengths of all of the sampled fish were known, it would be simple to simulate the parameters of the length-given-age model (since this is just a linear model). It would also be relatively simple to simulate the parameters of the proportion-at-age model (although the inclusion of random effects complicates the simulations somewhat). Also, parameters from the different submodels (age model, length-given-age model, and weight-given-length model) are independent in this case. (*ii*) If the parameters of the length-given-age model and the proportion-at-age model are known, it is simple to simulate the ages of the fish with only length data (since age-given-length is multinomial). (*iii*) We therefore treat the missing ages as parameters and use Gibbs sampling to alternate between simulating the missing ages and simulating the other model parameters. It is also possible to use block updating for most of the parameters apart from the precisions.

Using this approach, it is possible to find the joint posterior distribution of all of the parameters very quickly. On a reasonably powerful computer, 1 year's data can easily be analysed in less than 5 min. Obviously, the time increases with the number of years of data, but even 8 years worth takes under an hour. Convergence of the MCMC chains is fast because of the block-updating. Research is currently underway to make this even more efficient.

Estimating catch-at-age

We need to estimate the total catch-at-age a in cell c, T_{ca}. To take the uncertainty of the parameters into account, parameters (including random effects for cell and for those hauls that are observed) are samples from the joint posterior distribution (as described in the previous section). Given the parameters in the model, it can be shown that this is a simple function of those parameters (see below). Denoting one set of such parameters by θ, the total catch-at-age given the parameters can be written as a function $T_{ca}(\theta)$ of θ. A Monte Carlo estimate of the catch-at-age is then given by the mean of the $T_{ca}(\theta)$s. Uncertainty measures can be calculated simultaneously, i.e., standard errors are estimated by empirical standard errors of the $T_{ca}(\theta)$s.

Consider now the calculation of $T_{ca}(\theta)$ for a given set of parameters θ. We have $T_{ca} = T_c \times \text{mean}_c(p(a))$, where T_c is the total catch in the cell in numbers of fish and $\text{mean}_c(p(a))$ is the mean proportion-at-age over all hauls in the cell (i.e., the mean over all hauls taken by all boats fishing in that cell, not just those observed). We assume that there are a large number of these hauls so that the mean is equal to the expected value, giving us $T_{ca} = T_c E_c(p(a))$.

The total catch in a cell, W_c, is given in weight rather than numbers. We therefore need the mean weight of fish caught in the cell, $\bar{w}_c$, to calculate $T_c = W_c / \bar{w}_c$. We have

$$\log(\text{weight}_{c,h,f}) = \delta_{0,c,h} + \delta_1 \log(\text{length}_{c,h,f}) + \nu^{\text{fish}}_{c,h,f}$$

$$\log(\text{length}_{c,h,f}) = \beta_{0,c,h} + \beta_1 \log(\text{age}_{c,h,f}) + \varepsilon^{\text{fish}}_{c,h,f}$$

Thus:

$$\begin{aligned}\log(\text{weight}_{c,h,f}) &= \delta_{0,c,h} + \delta_1(\beta_{0,c,h} + \beta_1 \log(a_{c,h,f}) \\ &\qquad + \varepsilon^{\text{fish}}_{c,h,f}) + \nu^{\text{fish}}_{c,h,f} \\ &= \delta_{0,c,h} + \delta_1\beta_{0,c,h} + \delta_1\beta_1 \log(a_{c,h,f}) \\ &\qquad + (\delta_1 \varepsilon^{\text{fish}}_{c,h,f} + \nu^{\text{fish}}_{c,h,f}) \\ &= A_c + A_h + \beta_c \log(a_{c,h,f}) + C_f\end{aligned}$$

Here, A_c and B_c are constant for all hauls in a cell and given from the simulations, A_h is an unknown random haul dependent intercept, and C_f is an unknown random fish effect. From the earlier equations:

$$\begin{aligned}A_c &= (\delta^{\text{base}} + \delta^{\text{year}}_y + \delta^{\text{season}}_s + \delta^{\text{gear}}_g + \nu^{\text{region}}_r + \nu^{\text{cell}}_c) \\ &\quad + \delta_1(\beta^{\text{base}} + \beta^{\text{year}}_y + \beta^{\text{season}}_s + \beta^{\text{gear}}_g + \varepsilon^{\text{region}}_r + \varepsilon^{\text{cell}}_c)\end{aligned}$$

$$B_c = \delta_1\beta_1$$

A_h is a random haul dependent intercept:

$$A_h = \nu^{\text{haul}}_{c,h} + \delta_1 \varepsilon^{\text{haul}}_{c,h}$$

This is constant in a haul but a Gaussian random variable within a cell:

$$A_h \sim N\left(0, \frac{1}{\tau^{\text{haul}}_{\text{weight}}} + \frac{\delta_1^2}{\tau^{\text{haul}}_{\text{length}}}\right)$$

C_f is a random fish effect:

$$C_f = \delta_1 \varepsilon^{\text{fish}}_{c,h,f} + \nu^{\text{fish}}_{c,h,f}$$

This is a random fish effect, with a constant distribution:

$$C_f \sim N\left(0, \frac{1}{\tau^{\text{fish}}_{\text{weight}}} + \frac{\delta_1^2}{\tau^{\text{fish}}_{\text{length}}}\right)$$

Hence, the weight of a random fish f of age $a_{c,h,f}$ in haul h, cell c, is lognormal:

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$$\log(\text{weight}_{c,h,f}\,|\,a_{c,h,f}) \sim N\left(A_c + A_h + B_{c,a}\log(a_{c,h,f}), \frac{1}{\tau^{\text{fish}}_{\text{weight}}} + \frac{\delta_f^2}{\tau^{\text{fish}}_{\text{length}}}\right)$$

Its expectation (over all fish in the haul) is

$$E_{c,h}(\text{weight}_{c,h,f}\,|\,a_{c,h,f}) = \exp[A_c + B_c\log(a_{c,h,f})] \times \exp(A_h)\exp\left[\tfrac{1}{2}\left(\frac{1}{\tau^{\text{fish}}_{\text{weight}}} + \frac{\delta_f^2}{\tau^{\text{fish}}_{\text{length}}}\right)\right]$$

Taken over all hauls in a cell, this expectation is itself a random variable, also lognormal, since $\exp(A_h)$ is lognormal:

$$\log(E_{c,h}(\text{weight}_{c,h,f}\,|\,a_{c,h,f})) \sim N\left(A_c + B_c\log(a_{c,h,f}) + \tfrac{1}{2}\left(\frac{1}{\tau^{\text{fish}}_{\text{weight}}} + \frac{\delta_f^2}{\tau^{\text{fish}}_{\text{length}}}\right), \frac{1}{\tau^{\text{haul}}_{\text{weight}}} + \frac{\delta_f^2}{\tau^{\text{haul}}_{\text{length}}}\right)$$

The expected weight of a fish of age a in a cell is therefore

$$E_c(\text{weight}\,|\,a) = \exp\left[A_c + B_c\log(a) + \tfrac{1}{2}\left(\frac{1}{\tau^{\text{fish}}_{\text{weight}}} + \frac{\delta_f^2}{\tau^{\text{fish}}_{\text{length}}}\right) + \tfrac{1}{2}\left(\frac{1}{\tau^{\text{haul}}_{\text{weight}}} + \frac{\delta_f^2}{\tau^{\text{haul}}_{\text{length}}}\right)\right]$$

Again assuming a large number of hauls in a cell so that the mean weight-at-age is equal to its expected value, the mean weight of a fish in the cell is given by

$$\bar{w}_c = \sum_a E_c(p(a))\,E_c(\text{weight}\,|\,a)$$

There is no explicit formula for $E_c(p(a))$, but the estimator

$$\hat{E}(p(a)) = \frac{\exp[E_c(\alpha^a_{c,h})]}{\sum_{a'=1}^{A}\exp[E_c(\alpha^{a'}_{c,h})]}$$

is almost unbiased, so long as the within-cell variance of $\alpha^a_{c,h}$ for each age is small compared with the difference between the $E(\alpha^a_{c,h})$ for the different ages within the cell. This is certainly the case for our data.

Results

The model can be fitted in about 30 min for 8 years of data on a modestly powerful computer. We take every tenth sample from an MCMC run of 10 000, after a burn-in of 1000 samples. There are no problems with convergence, and the thinning removes the serial correlation in the samples. We obtain as output the joint posterior distribution of total catch for each age group for any combination of cells as well as the (joint) posteriors of all the individual parameters. We expect that interest will usually be mostly in the catch-at-age results, along with the uncertainty in the estimates, which is directly available from the posteriors. One example of these results is shown (Fig. 3) where the posterior means for each age, along with 95% credible intervals, are plotted for 1995 and 2002 using data from 1995 to 2002. Obviously, the 12 age groups are not independent, but the error bars give a good indication of the uncertainty. If, for example,

Fig. 3. Estimates of catch-at-age in (*a*) 1995 and (*b*) 2002 using only *Amigo* data (crosses) and all data (circles). Bars are 95% credible intervals.

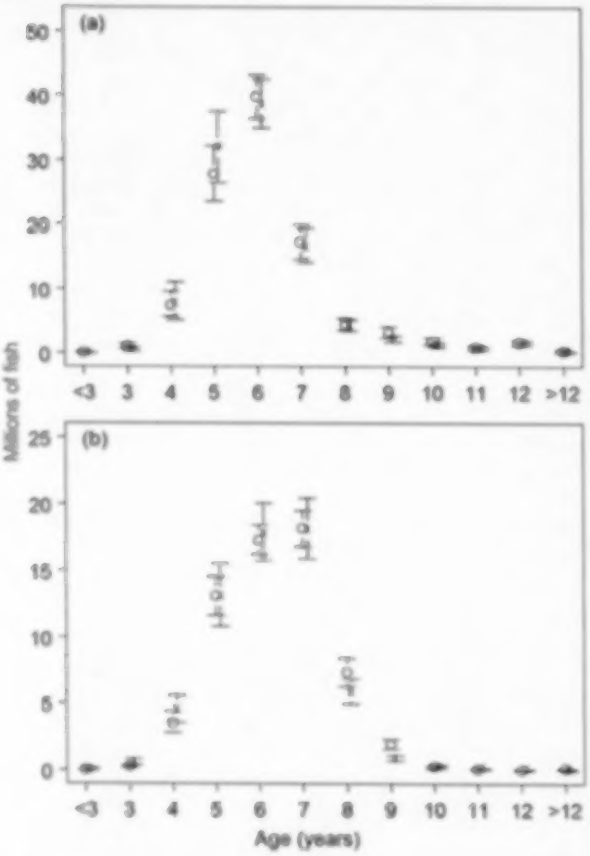

Fig. 4. Numbers of *Amigo* hauls (crosses) and extra hauls (circles) sampled in each year.

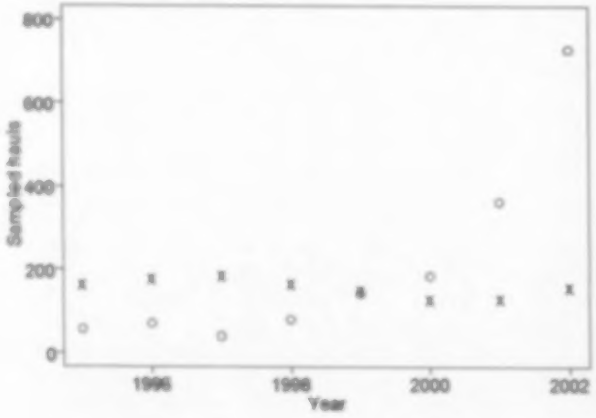

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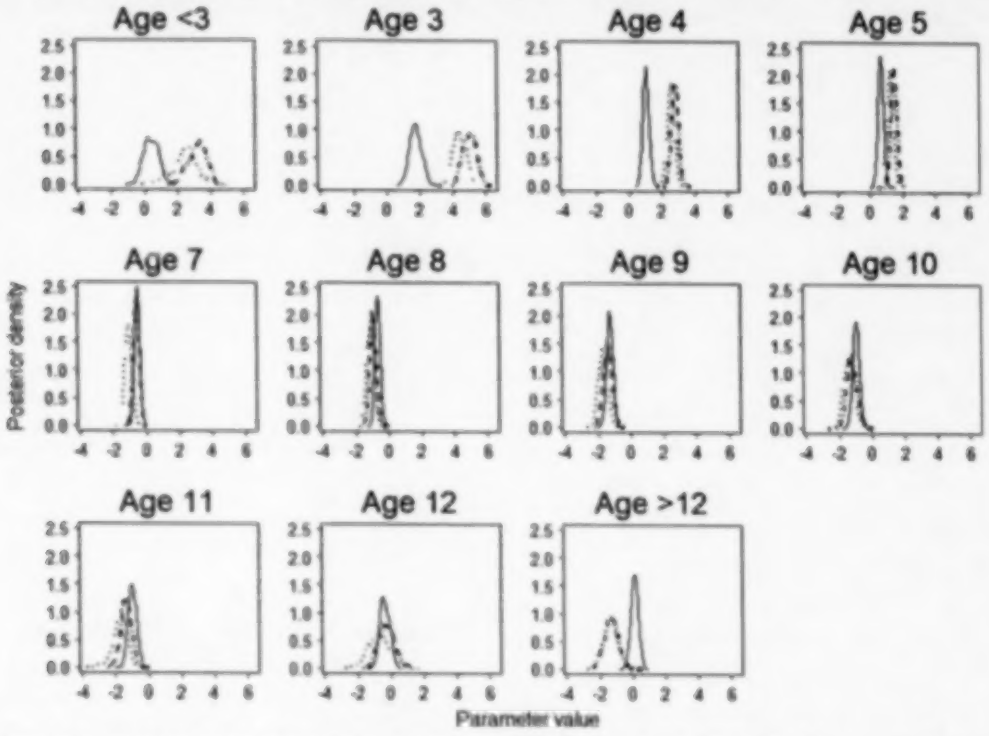
Fig. 5. Posterior distributions of the standard deviations of the random effects in the proportion-at-age model. Solid line, area standard deviation; dotted line, haul standard deviation; dot-dashed line, cell standard deviation.

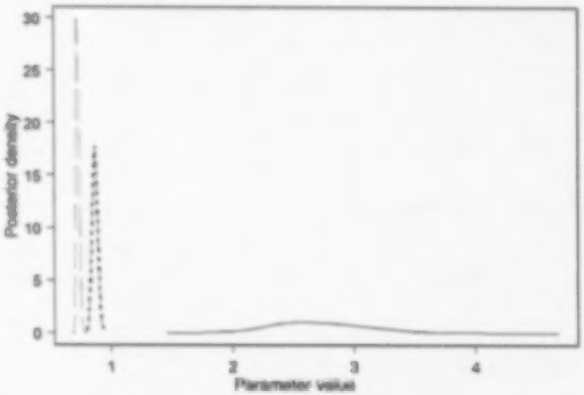


the results were to be used for a virtual population analysis, samples from the full joint posteriors for all required years would be available. These could be used to obtain the posterior distributions of the parameters calculated in the virtual population analysis.

These plots also illustrate the effect of using the length-only data in addition to the length and age data from the *Amigo*. The numbers of *Amigo* and extra (i.e., reference fleet and Coast Guard) hauls sampled per year are shown in Fig. 4. The extra samples are virtually all length only, although it is expected that in the future, there will be more age-given-length samples. In 1995, there were only about 50% as many extra samples as *Amigo* samples, and there is almost no difference in the results. By 2002, however, there were about four times as many extra as *Amigo* samples, and there is a useful reduction in the size of the error bars. Also, some of the point estimates have moved outside the *Amigo*-only intervals.

The model parameters are also of interest, and we show some examples in Figs. 5 and 6. The first (Fig. 5) shows the posterior distributions of standard deviations of the random effects in the age model, i.e., $\sqrt{1/\tau_{age}^{cell}}$, $\sqrt{1/\tau_{age}^{haul}}$, and $\sqrt{1/\tau_{age}^{region}}$. The region standard deviation is the most uncertain, not surprisingly, since we only use eight regions in its estimation. The haul standard deviation is the most precisely estimated. Note that the region standard deviation should be scaled by the number of neighbours of a region in the distribution of $\zeta_{sr}^{region,\sigma}$, and so, for a region with several neighbours, the posterior mean of the standard deviation would in fact be smaller than the posterior means of the other two standard deviations. It is difficult to make any useful interpretation of these parameters, except to see which are well or badly estimated.

Fig. 6. Posterior distributions of the season effects in the proportion-at-age model. Solid line, season 2; dotted line, season 3; dot-dashed line, season 4. Season 1 is defined to be zero.



The second example (Fig. 6) shows the posterior means of the season effects in the age model (i.e., $\alpha_s^{season,\sigma}$). Note that the values for age 6 and season 1 are defined to be zero. A high value for this parameter means a higher probability of catching fish from age group a in season s. Take, for example, the first plot (age < 3). The value for season 1 is defined to be zero. The mean for season 2 (solid line) is slightly greater than zero; the mean for season 3 (dotted line) is big-

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ger again, and for season 4 (dot-dashed line), it is even bigger. Thus, the proportion of this age group in the catch increases with season. This may be because the fish get significantly bigger. This effect can be seen to a lesser degree for ages 3 and 4, but it disappears, or maybe even reverses, for older fish.

Discussion

The model described is as far as we know the first comprehensive approach to analysing multiple sources of catch-at-age data, in a way that can include all types of sampling schemes that we know of. It is explicit in its assumptions and given these assumptions properly accounts for the uncertainty in the estimation. It is very fast (at least compared with traditional methods) and in addition to the catch-at-age estimates can also give information on the model parameters, which may be interesting biologically.

We have shown herein that adding length-only samples to the age samples improves the precision of the catch-at-age estimates. The relatively small improvement even with a large sample of lengths reflects the relative lack of information in these samples. One very useful function of our model would be to explore the effect of adding more length samples or changing the sampling strategy in some other way. It would be possible to simulate from the model and investigate any desired changes in numbers and locations of samples. We hope to do this in a later paper.

There are a number of additions and improvements that could be made. Perhaps the most interesting would be to include errors in the age reading. This was done for the simpler sampling scheme of Hirst et al. (2004) and with some development could be included in this model. This may be important because unpublished work from the IMR suggests that on average, about 10% of the ages of cod may be wrong by 1 year, increasing up to 40% for older fish. It would also be possible to include different length-given-age or weight-given-length models, which may be appropriate for different fish species, or a different spatial model that may suit different fisheries.

Acknowledgements

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Appendix A. Details of the model.

In all three models (proportion-at-age, length-given-age, and weight-given-length), the fixed effect parameter values are relative to the baseline terms $\alpha^{base,a}$, β^{base}, and δ^{base}, and it is necessary to set one level of each fixed effect to zero for identifiability:

$$\alpha^{year,a}_{y^\circ} = \alpha^{season,a}_{s^\circ} = \alpha^{gear,a}_{g^\circ} = \beta^{year}_{y^\circ} = \beta^{season}_{s^\circ} = \beta^{gear}_{g^\circ} = \delta^{year}_{y^\circ} = \delta^{season}_{s^\circ} = \delta^{gear}_{g^\circ} = 0$$

For the proportion-at-age model, the proportions must sum to 1, and so we have the additional restriction that all parameters for one age group a° are set to zero:

$$\alpha^{base,a^\circ} = \alpha^{year,a^\circ}_{y} = \alpha^{season,a^\circ}_{s} = \alpha^{gear,a^\circ}_{g} = 0$$

We use $a^\circ = 6$ (usually the most common age group) and $y^\circ = s^\circ = g^\circ = 1$. The choice of y°, s°, and g° is unimportant, but convergence is fastest if a° is one of the most common age groups. Setting the parameters to zero for some value of a° has the undesirable effect of giving the catch-at-age for this age group a smaller posterior variance than for the other age groups. A better restriction might be to make the mean over all age groups constant.

We give all nonzero fixed effects noninformative prior distributions:

$$\alpha^{base,a} \sim N(0,1/0.001)\,\forall\, a \neq a^\circ$$

$$\alpha^{year,a}_{y} \sim N(0,1/0.001)\,\forall\, y \neq y^\circ, a \neq a^\circ$$

$$\alpha^{season,a}_{s} \sim N(0,1/0.001)\,\forall\, s \neq s^\circ, a \neq a^\circ$$

$$\alpha^{gear,a}_{g} \sim N(0,1/0.001)\,\forall\, g \neq g^\circ, a \neq a^\circ$$

and so on for the β and δ terms.

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The spatial terms $\zeta_r^{\text{region},a}$, $\varepsilon_r^{\text{region}}$, and ν_r^{region} have Gaussian conditional autoregressive prior distributions (e.g., see Carlin and Louis 1996):

$$\zeta_r^{\text{region},a^*} = 0$$

$$\zeta_r^{\text{region},a^*} \left| \zeta_{j\neq r}^{\text{region},a} \sim N\left(\overline{\zeta}_r^{\text{region},a}, \frac{1}{\tau_{age}^{\text{region}} n_r} \right), \quad a \neq a^* \right.$$

$$\overline{\zeta}_r^{\text{region},a} = n_r^{-1} \sum_{j \in \partial(r)} \zeta_j^{\text{region},a}$$

where $\partial(r)$ is the set of neighbours of region r and n_r is the number of neighbours of region r.

The priors for $\varepsilon_r^{\text{region}}$ and ν_r^{region} are similar.

The ζ, ε, and ν terms are independent random effects, again set to zero for $a = a^*$, with the following priors:

$$\zeta_c^{\text{cell},a} \sim N(0, 1/\tau_{age}^{\text{cell}}) \forall\, c, a \neq a^*$$

$$\zeta_h^{\text{haul},a} \sim N(0, 1/\tau_{age}^{\text{haul}}) \forall\, h$$

$$\zeta_c^{\text{cell},a^*} = \zeta_h^{\text{haul},a^*} = 0 \forall\, c, h$$

The ε and ν priors are similar. All precision terms τ are given vague Gamma(0.01,0.01) priors.

A sensitivity analysis showed no effect of varying the priors. It is known that in some models, the choice of prior for the precision terms can be very influential on the results, but in our case, this is not true. The reason for this is probably that there are only a relatively small number of precisions to estimate, and there is a large amount of data. The only noticeable effect of varying the precision priors between Gamma(0.1,0.1) and Gamma(0.001,0.001) was to slow the sampling routine down somewhat for the vaguest priors.

Note that throughout the paper, we have parameterized the Gaussian distributions in terms of the precision (i.e., the reciprocal of the variance), i.e., we write $N(\mu, 1/\tau)$ rather than, for example, $N(\mu, \sigma^2)$. This is the usual Bayesian notation used for algebraic simplicity because we usually give τ a Gamma prior distribution.

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Appendix B. Markov Chain Monte Carlo (MCMC) algorithm.

Denote by θ_{age}, θ_{lga}, and θ_{wgl} the set of parameters involved in the age, length-given-age, and weight-given-length model, respectively. Our goal is to simulate from the posterior distribution $p(\theta_{age}, \theta_{lga}, \theta_{wgl} | \text{data})$. Note first that

$$p(\theta_{age}, \theta_{lga}, \theta_{wgl} | \text{data}) = p(\theta_{age}, \theta_{lga} | \text{data}) p(\theta_{wgl} | \text{data})$$

so that simulation of θ_{wgl} can be performed separately from $(\theta_{age}, \theta_{lga})$. In the current implementation, the simulation of θ_{wgl} is performed using Gibbs sampling by sequentially altering between the following steps:

(*i*) Simulate fixed effects conditional on random effects, precision parameters, and data.

(*ii*) Simulate random effects conditional on fixed effects, precision parameters, and data.

(*iii*) Simulate precision parameters conditional on fixed effects, random effects, and data.

Since this part of the model is an ordinary regression model (with random effects), each step can be performed by standard methods (e.g., see Gelman et al. 1995, chap. 8).

Concerning the simulation of $(\theta_{age}, \theta_{lga})$, note that these two sets of variables become dependent because of the length-only data. Denote by a_{miss} the set of missing ages corresponding to the length-only data. Simulation of $(\theta_{age}, \theta_{lga})$ is performed through the following three main steps:

(*i*) Simulate the missing ages a_{miss} conditional on $(\theta_{age}, \theta_{lga})$ and data.

(*ii*) Simulate θ_{age} conditional on θ_{lga}, a_{miss}, and data.

(*iii*) Simulate θ_{lga} conditional on θ_{age}, a_{miss}, and data.

Given $(\theta_{age}, \theta_{lga})$, all missing ages are independent multinomial variables, making them easy to draw.

For given a_{miss}, the length-given-age model is a standard regression model similar to the weight-given-length model and simulation of θ_{lga} can be performed as for θ_{wgl}. The simulation of θ_{age} is more difficult owing to the nonlinear dependence between data and parameters. In the current implementation, simulation of θ_{age} is performed through the following two main steps:

(*i*) Simulate the $\alpha_{c,h}^a$ given the rest of θ_{age} and data.

(*ii*) Simulate the rest of θ_{age} given the $\alpha_{c,h}^a$ and data.

Given the rest of θ_{age}, all $\alpha_{c,h}^a$ are independent and can be simulated through Metropolis–Hastings steps. Given the $\alpha_{c,h}^a$, the rest of the age model can be considered as a standard regression model and simulation of the remaining parameters can be performed similar to the simulation of θ_{lga} and θ_{wgl}.

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Variation of Y-chromosome DNA markers in Chinook salmon (*Oncorhynchus tshawytscha*) populations

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Abstract: Two Y-chromosome DNA markers (a repetitive sequence, OtY1, and a single-copy marker, GH-Y) tightly linked to the sex-determination locus have been examined for their association with sexual development among 55 populations of Chinook salmon (*Oncorhynchus tshawytscha*) from the Yukon, British Columbia, Washington, Oregon, and Idaho. Normal linkage has been observed in 96.7% of 2478 individuals examined. Only five males (0.44%) were found lacking both markers (none from Canadian systems), and 14 females (1.04%) from US populations and two females (0.15%) from Canadian populations were found to possess both markers. Variants identified included weakly amplifying alleles for GH-Y and OtY1 and structural variants identified by Southern-blot analysis. The frequency of variants in males was more than 2-fold that in females, and males deficient in GH-Y were more common (3.6%) than males deficient in the repetitive OtY1 sequence (0.7%). Some individuals (of both sexes) possessed fewer copies of the OtY1 repeat than normal males, revealing molecular dynamics that alter Y-chromosome structure within and among populations. A population (Hanford Reach) previously reported as having a high incidence of females possessing the OtY1 marker, and suspected of being sex-reversed, was found to have normal sex-marker genotypes in the present study.

Résumé : Nous avons examiné l'association entre deux marqueurs ADN du chromosome Y (une séquence répétitive, OtY1, et un marqueur à copie unique, GH-Y), intimement liés au locus de la détermination du sexe, et la maturation sexuelle chez 55 populations de saumons chinook (*Oncorhynchus tshawytscha*) du Yukon, de la Colombie-Britannique, du Washington, de l'Oregon et de l'Idaho. Il existe une liaison normale dans 96,7 % des 2478 individus examinés. Seuls cinq mâles (0,44 %, aucun ne provenant des eaux canadiennes) ne possèdent ni l'un ni l'autre marqueur; 14 femelles (1,04 %) des É.-U. et deux femelles (0,15 %) du Canada possèdent les deux marqueurs. Les déviations observées incluent des allèles à faible amplification de GH-Y et OtY1 et des variations structurales identifiées par analyse de buvardage de Southern. Les déviations sont deux fois plus communes chez les mâles que chez les femelles et les mâles porteurs d'une déficience à GH-Y (3,6 %) sont plus nombreux que ceux qui ont une déficience au séquence répétitif OtY1 (0,7 %). Quelques individus (des deux sexes) possèdent un nombre plus petit de copies de la répétition OtY1 que les mâles normaux, ce qui indique qu'il y a une dynamique moléculaire qui modifie la structure du chromosome Y à l'intérieur des populations et d'une population à l'autre. Une population (de Hanford Reach), signalée dans le passé pour avoir une fréquence élevée de femelles porteuses du marqueur OtY1 et soupçonnée d'avoir une inversion sexuelle, possède dans notre étude des génotypes normaux quant aux marqueurs sexuels.

[Traduit par la Rédaction]

Introduction

The sex chromosomes of many species are morphologically differentiated to the degree where they can be distinguished cytogenetically. This structural divergence arises from molecular differences in the form of mutational degeneration of functional genes, large deletions or additions of non-coding repetitive sequences, and transposable element insertions that accumulate between the sex chromosomes in the heterogametic sex (Carrozzo et al. 1992; Steinemann 1992; Tilford et al. 2001). Complex evolutionary mechanisms drive this divergence, which primarily occurs in the vicinity of sex chromosomes that are in tight genetic linkage with the sex-determination locus (Kirpichnikov 1981; Charlesworth 1991; Rice 1996). This region of sex chromosomes is transmitted within a single sex and thus cannot become homozy-

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gous in natural populations; consequently, recessive genetic damage that has arisen near the sex-determination locus is selected against less effectively than for autosomal regions. Thus, genetic alterations are more able to accumulate, particularly if the movement of such mutations into populations is facilitated by reduced recombination, Muller's ratchet (Felsenstein 1974; Muller 1964), or hitchhiking with high-fitness alleles or dosage compensation (Muller 1932; Lucchesi 1978; Charlesworth 1996).

In fish, only approximately 10% of species possess cytogenetically distinguishable XY or ZW sex chromosomes (Arkhipchuk 1995; Devlin and Nagahama 2002). Other species utilize polyfactorial or environmental modes of sex determination (Yamamoto 1969; Baroillier et al. 1999; Devlin and Nagahama 2002), and others, based on genetic evidence, appear to possess sex chromosomes that cannot be distinguished cytogenetically. This suggests that in some cases, the sex-limited region of these chromosomes may be relatively small (the differential region), with the remainder behaving as a pseudoautosomal chromosomal region (Kirpichnikov 1981; Rice 1996). A small differential region between the X and Y chromosomes in association with the sex-determination locus may represent an early stage of sex-chromosome evolution, and might arise from frequent changes in sex-determination mechanisms in fish, owing to the lability of their sex-control mechanisms and (or) to frequent rearrangements associated with the sex chromosomes (reviewed in Devlin and Nagahama 2002). Woram et al. (2003) have clearly shown that among salmonid species, the sex-determination region is located on different linkage groups, indicating that significant chromosome-level rearrangement of this locus has occurred.

Molecular characterization of fish sex chromosomes has allowed isolation of DNA sequences tightly linked to the sex-determination locus from several species, including *Poecilia reticulata* (Nanda et al. 1992), *Leporinus elongatus* (Nakayama et al. 1994), *Xiphophorus maculatus* (Coughlan et al. 1999), *Oryzias latipes* (Matsuda et al. 1997), *Gasterosteus aculeatus* (Griffiths et al. 2000), *Oncorhynchus mykiss* (Iturra et al. 1998), and salmon species (Devlin et al. 1991; Du et al. 1993; Forbes et al. 1994). Recently, the gene responsible for sex determination in medaka has been cloned (Matsuda et al. 2002; Nanda et al. 2002). However, very little information currently exists concerning the level of variation in sex-specific markers among individuals and populations of fish species.

Pacific salmonids possess an XY system of sex determination, but only limited cytogenetic differences are apparent (Thorgaard 1977, 1978; Ueda and Ojima 1984*b*), indicating that the differential region between the sex chromosomes is relatively small. Indeed, YY individuals have been shown to be viable and fertile for rainbow trout (Chevassus et al. 1988; Scheerer et al. 1991) and Chinook salmon (Devlin et al. 2001), indicating that no vital genes have been deleted from the Y chromosome during its evolution. Nevertheless, some molecular differences have been identified between the X and Y chromosomes in salmonids that are not revealed at the cytogenetic level. For Chinook salmon (*Oncorhynchus tshawytscha*), OtY1 is a sequence which is part of an 8-kilobase (kb) repeat (OtY8) that is organized in a direct tandem fashion approximately 300-fold on the Y chromosome (Devlin et al. 1991, 1994*a*, 1998). A second sequence (Clifton and Rodriguez 1997) has also been independently isolated which is a subfragment from within the OtY8 repeat (R.H. Devlin, unpublished data). The OtY8 repeats are organized into six major genomic clusters spanning some 2–3 Mb in size, all of which appear to be genetically closely linked to the sex-determination locus and map by in-situ hybridization to a single region on the tip of an acrocentric Y chromosome (Stein 2001). A second marker, GH-Y, is a growth-hormone sequence that is located near the sex-determination locus on the Y chromosome of Chinook (Du et al. 1993), coho (*Oncorhynchus kisutch*) (Forbes et al. 1994), pink (*Oncorhynchus gorbuscha*) (Devlin et al. 2001), chum (*Oncorhynchus keta*) (Devlin et al. 2001), and masu (*Oncorhynchus masou*) salmon (Nakayama et al. 1999; Zhang et al. 2001). This locus appears to be derived from the autosomal *GH-2* gene, having the characteristics of a nonfunctional pseudogene, based on genetic damage to the regulatory and coding regions of the gene (Du et al. 1993).

Although the GH-Y and OtY1 markers are usually restricted to males, some evidence has been recently presented that has identified exceptions to the Y-chromosome linkage of GH-Y and OtY1 markers in two salmonid species (Nagler et al. 2001; Zhang et al. 2001; Williamson and May 2002). Chinook salmon were examined for one of the Y-chromosome markers (OtY1) in a wild population in the Columbia River (Nagler et al. 2001) and in several populations in California (Williamson and May 2002), and phenotypic females possessing this male marker were found in both investigations at high (84%) and moderate (up to 38%) frequencies, respectively. The possibility that extensive sex reversal was occurring was suggested in both studies. In masu salmon and sister-species, the frequency of exceptions identified was quite low (Zhang et al. 2001), but sex reversal or recombination between the sex chromosomes were also considered possible explanations. Here we present a summary of the distribution of the OtY1 and GH-Y markers and variants determined over the past 15 years for male and female adult salmon from populations of Chinook salmon from British Columbia and the Yukon in Canada, and from Washington, Oregon, and Idaho states in the USA.

Materials and methods

Fish and tissue collections

Chinook salmon eggs and sperm were collected from fish from the Chilliwack River, and a single-pair cross was performed. Progeny were reared in fresh water in the West Vancouver Laboratory hatchery for 9 months, at which time they were euthanized with an overdose of tricaine methanesulfonate (MS 222), dissected, and examined for gonadal type. Following caudal sever with a new razor blade for each fish, 2 μL of blood was collected from each individual and lysed by vortexing in 100 μL of 0.01 mol·L^{-1} NaOH, followed by incubation at 95 °C for 5 min. Following centrifugation, 2 μL was used as template in 50 μL polymerase chain reactions (PCR) (see below).

Adult salmon, collected since 1989, were sampled from natural, hatchery-reared, or captive-brood populations and sexed by internal identification of the gonad type, and a tissue (liver or fin) or blood sample was removed. Extreme

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Table 1. Linkage of GH-Y and OtY1 sequences and gonadal sex phenotype in F_1 progeny of a single-pair cross of Chilliwack River Chinook salmon (*Oncorhynchus tshawytscha*).

	GH-Y –		GH-Y +		
	OtY1 –	OtY1 +	OtY1 –	OtY1 +	χ^2 P^a
Ovary	50	0	0	0	0.888
Testis	0	0	0	50	

[a]Probability that the sex ratio does not differ from 1:1.

care was taken in identifying the gonadal type of each fish and subsequent labeling of sample tubes, since there was usually no opportunity to reexamine gonadal phenotypes in any exceptional individuals that might be discovered. Liver and fin samples were stored in 100% non-denatured ethanol and DNA templates prepared using K-buffer extractions (Kawasaki 1990), or DNeasy Tissue kits (Qiagen). Blood samples were collected by caudal puncture or sever, and 15 µL was added to 1 mL of 100% ethanol for long-term storage, and 2 µL was lysed in NaOH as described above.

PCR and Southern-blot analysis

PCRs for the OtY1 and GH-Y loci were carried out essentially as described in Du et al. (1993) and Devlin et al. (1994*b*, 2001). Primers OtY1 and OtY2 (Devlin et al. 1994*b*) were utilized to amplify the OtY1 locus and products were analyzed on 2% agarose gels stained with ethidium bromide. For detection of GH-Y, primers GH5 and GH6 (Devlin 1993) or primers F and G were utilized (Du et al. 1993; Devlin et al. 2001). GH-Y alleles were analyzed on 0.8% agarose gels. In some cases, OtY1 and GH-Y loci were amplified using fluorescently labeled primers and analyzed by capillary electrophoresis using POP-4 polymer on an Applied Biosystems 310 Genetic Analyzer. All exceptions were reanalyzed at least once to confirm their genotype, and in the case of females possessing Y-chromosome-linked markers, new DNA extractions were performed from tissues and reassayed.

Template DNA preparation and digestion, probe labeling, and Southern blotting were performed essentially as described in Devlin et al. (1991, 2001). The OtY1 locus was analyzed using a probe generated from cloned OtY1, whereas the GH-Y locus was detected using a probe (GH2-8) consisting of coding sequence from the salmon GH-2 gene (Devlin 1993).

Results

Two Y-chromosome DNA markers (GH-Y and OtY1) have been examined in male and female individuals from a family cross and from natural, hatchery-reared, and captive populations of Chinook salmon to examine the linkage conservation between these markers and the male sex-determination locus on the Y chromosome.

Family analysis

To examine how tightly linked genetically the DNA sequence markers are with the sex-determination region of the Y chromosome, a family cross for Chinook salmon was produced, and segregation of the GH-Y and OtY1 loci to sons or daughters was examined. The father possessed both Y-chromosome markers, and 100 progeny were dissected at 9 months of age and visually examined for the presence of ovary or testis, and a blood sample was taken for PCR analysis. The phenotypic sex ratio did not significantly differ from 1:1 within the cross ($P = 0.888$, $\chi^2 = 0.02$, 1 df), and both OtY1 and GH-Y sequences were identified in all F_1 males but not in any F_1 females (Table 1). These results indicate that these loci are genetically closely linked (less than 1 centimorgan (cM)) to the sex-determination locus on the Y chromosome in Chinook salmon.

Survey of adult salmon

A survey of mature adult Chinook salmon from the Yukon, British Columbia, Washington, Oregon, and Idaho (Fig. 1) was undertaken to examine how conserved the Y-chromosome linkage of OtY1 and GH-Y was among populations. Chinook salmon ($n = 2478$) from 55 populations from these regions were examined.

Males

Among 1139 males examined, 1095 (96.1%) possessed both GH-Y and OtY1 markers (Appendix A). Eight males (0.7%) among 7 populations were missing the OtY1 marker (none in the Canadian systems), and 41 males (3.6%) distributed among 14 populations were missing the GH-Y marker. However, additional variants were observed among males: 37 individuals among six populations were found to have weakly amplifying OtY1 signals (OtY1MF; Fig. 2*a*), and 25 individuals among seven populations were found to have a weakly amplifying GH-Y band (GH-Yw; Fig. 2*c*). The GH-Yw allele has greater than 95% sequence identity (data not shown) with the common GH-Y allele and thus is considered allelic. The overall frequency of all types of male variation was 6.9%, and a similar overall frequency of male variation was found in Canadian (6.2%) and US (8.6%) populations. Thirty-four (61.8%) populations showed no variation of sex linkage of the markers among males; however, the remaining exceptions did not appear to be randomly distributed among populations: no males lacking both markers were identified among 777 fish examined from Canadian populations, whereas 5 such exceptional males (1.38%) from five populations were identified among 362 US males, indicating a significant difference based on geographic origin ($P = 0.005$; $\chi^2 = 7.8$, 1 df). In Canadian systems, variants were clustered in central British Columbia coastal systems, central British Columbia populations, and one Vancouver Island population (Robertson Creek), whereas in the USA, variants were more evenly distributed among populations, although populations in the upper Columbia River appeared to have a somewhat higher proportion. Two notable populations were associated with high numbers of variants: the Kitimat River in central British Columbia possessed a large number of males with weakly amplifying alleles of both

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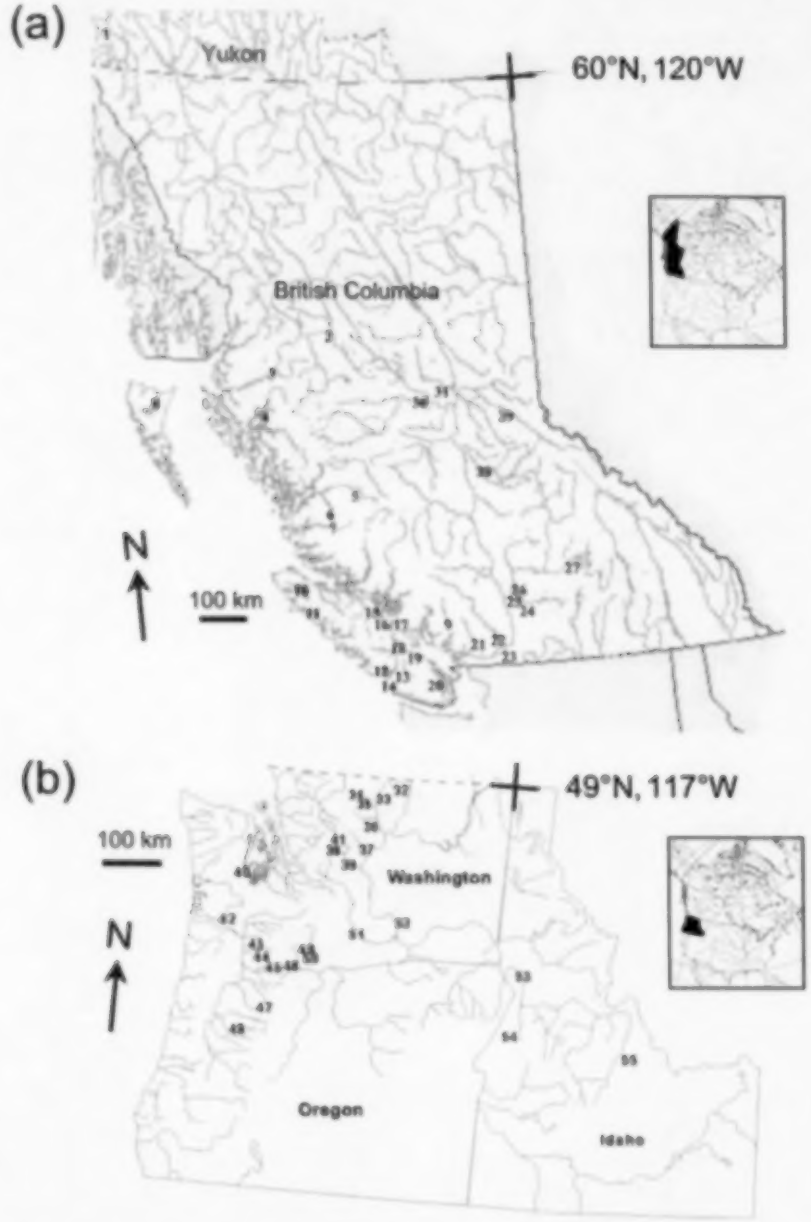
Fig. 1. Geographic locations of sources of Chinook salmon (*Oncorhynchus tshawytscha*) analyzed from the Yukon, British Columbia, Washington, Oregon, and Idaho. The numbers correspond to populations listed in Appendix A. The crosses indicate longitude and latitude reference points: (*a*) 60°N,120°W; (*b*) 49°N,117°W. Solid areas in inset maps show the location of sampled areas within North America.



markers, and W.F. Yankee Creek in Idaho contained many males deficient in the GH-Y marker.

Structural variation of Y-chromosome loci was examined by Southern-blot analysis. Southern blots of *Bam*HI-digested Chinook salmon DNA probed with OtY1 sequence produce primarily an intense band at 8 kb in males (Fig. 2*b*) derived from the extensive (approximately 300) tandem repeats (OtY8) associated with this locus (Devlin et al. 1991, 1994*a*, 1998). Both males and females possess additional bands as well, presumably derived from autosomal or X-chromosome-linked sequences with homology to the repeat, but in normal males these are present at a much reduced copy number relative to sex-linked OtY8 sequences and are not organized into 8-kb direct tandem arrays. In agarose gels, normal male DNA (with intense OtY8 repeat Southern-blot bands) supports intense PCR amplification of OtY1 (OtY1M band), whereas

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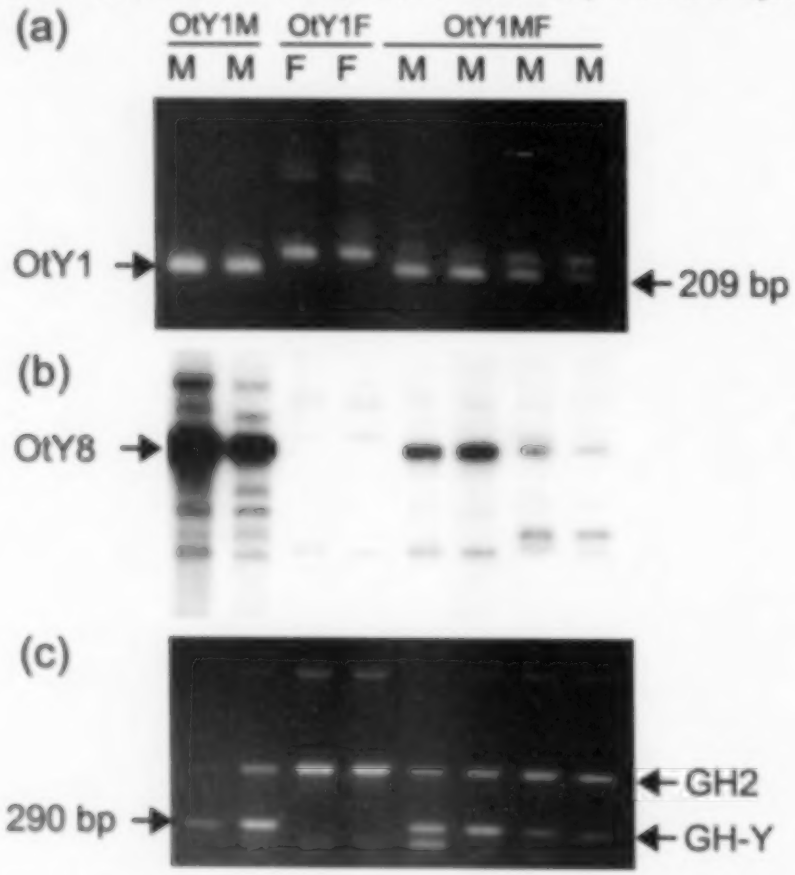
Fig. 2. Polymerase chain reaction (PCR) and Southern-blot analysis of OtY1 and GH-Y alleles in male Chinook salmon from the Lower Atnarko River (M, testis-containing fish; F, ovary-containing fish). In each panel, from left to right: two normal males (classified as OtY1M), two normal females (classified as OtY1F), and four males with weak OtY1 amplification (classified as OtY1MF). (*a*) Amplification with primers OtY1 and OtY2, showing, in lanes 1 and 2, strong amplification of the 209-bp OtY1M band in males (arrow), and in lanes 3 and 4, the absence of this band in females but with concomitant amplification of the larger female-prevalent bands (OtY1F) above, and in lanes 5–8, weak amplification of both the male and female bands in OtY1MF males. (*b*) Long exposure of a Southern blot of *Bam*HI-digested genomic DNA probed with OtY1 sequence, showing reduced signal for the male-specific 8-kb repeat band (OtY8, arrow) in OtY1MF males. (*c*) Amplification of the 290-bp male-specific GH-Y band (arrow), showing two males (far right) with weak amplification signals relative to the autosomal GH2 band immediately above. Note the presence of an additional non-sex-linked GH fragment (275 bp) immediately below the pseudogene band, which requires care to distinguish from GH-Y.



normal female DNA does not support detectable amplification of OtY1M but does yield alternate higher molecular weight bands (Fig. 2*a*). These "female" bands (OtY1F) can be detected in amplifications from male DNA using high-resolution capillary electrophoresis analysis of PCR reactions amplified with fluorescently labeled primers, but at much reduced intensity relative to those from females (Fig. 3*a*). This is consistent with OtY1 PCR reactions being a competition between templates from the Y-chromosome-linked repeats (present in high copy number in the genome) and fewer autosomal or X-chromosome-linked homologous sequences (Devlin et al. 1994*b*). When a high copy number of the OtY8 repeat is present, "female" sequences are out-competed and largely eliminated from the reaction and are not clearly visible. Some male DNA supports only weak amplification of OtY1 (OtY1MF), and in these cases, female bands are also amplified (Fig. 2*a*). These males also have a much-reduced signal for OtY8 on Southern blots (Fig. 2*b*), indicating that the Y-chromosome-linked repeat can be reduced in copy number in some exceptional males.

Other variants of OtY8 have also been identified by Southern-blot analysis: some males from the Babine River yield a weak OtY1 PCR signal, and these individuals possess a smaller (6 kb) repeat band in addition to the 8-kb band, which is found in reduced intensity (Fig. 4). These fish presumably contain a novel repeat class, which may be deleted for the OtY1/2 primer binding sites. Some fish within the Babine River system also possessed weakly amplifying alleles of GH-Y, but none of these individuals possess the 6-kb repeat class, suggesting that the two variants have arisen independently from normal Y chromosomes (with strong amplification of both OtY1 and GH-Y).

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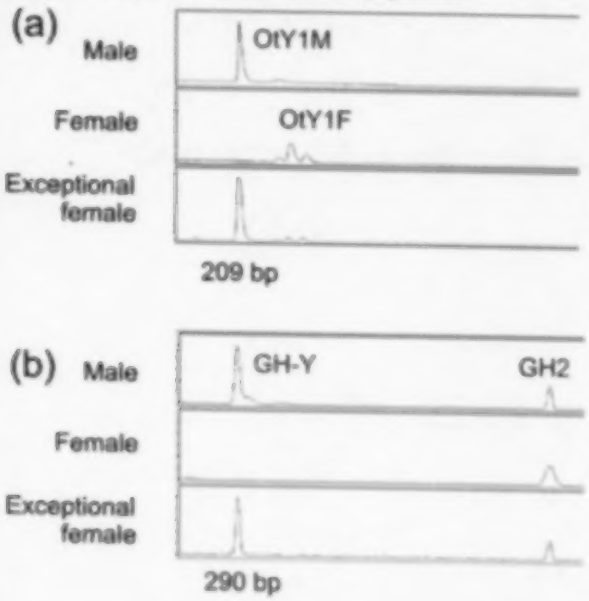
Fig. 3. Example of Y-chromosome markers in a male, a female, and an exceptional female by high-resolution capillary electrophoresis. (*a*) OtY1. (*b*) GH-Y. The *y*-axis values in each graph are arbitrary fluorescence levels with approximate scales of 0–1600 for graphs in *a* and 0–1000 for graphs in *b*.



Females

Of the 1339 female Chinook salmon examined from 54 populations, 1302 (97.2%) among 41 populations did not support detectable (in agarose gels) amplification of either the GH-Y or OtY1 marker (Appendix A, Figs. 2*a* and 2*c*) as expected if they were of normal XX genotype. Sixteen exceptional females (1.19%) from 10 separate populations possessed both the OtY1 and the GH-Y marker, although only 7 of these fish among five populations contained alleles that amplified with normal intensity (i.e., neither GH-Yw nor OtY1MF alleles). Of the 16 exceptional females possessing both markers, 14 were observed among 543 US female salmon examined (2.574%) and 2 among 796 Canadian female salmon examined (0.25%), indicating a significant ($P < 0.001$; $\chi^2 = 12.9$, 1 df) geographic difference in the distribution of variation in the region examined. The GH-Y and OtY1 signals in exceptional females comigrated with their respective bands from normal males analyzed by high-resolution capillary electrophoresis (Fig. 3). Other females exhibiting variation included (*i*) 11 fish (0.82%) that possessed the weakly amplifying GH-Yw allele but were negative for OtY1, (*ii*) 2 fish (0.15%) that possessed strong signals for OtY1 but were negative for GH-Y, (*iii*) 7 fish (0.52%) that were negative for GH-Y and amplified OtY1 weakly, and (*iv*) 1 fish (0.07%) that was completely deficient in OtY1 but possessed a normal GH-Y allele. A higher proportion of US streams (10/24) than Canadian systems (4/31) were associated with female variation. The Elochoman and Entiat systems were noted to contain a high proportion of female variation.

Southern-blot analysis of exceptional females positive for OtY1 revealed that they do possess OtY8 repeat sequences, but the copy number is variable among individuals, and is reduced relative to that observed in normal males (Fig. 5). OtY8 signals were also identified by random Southern-blot screening in one female from Robertson Creek identified as possessing the OtY1F allele by PCR analysis. The presence of some OtY8 repeats in females suggests that in rare cases these sequences are able to translocate or be exchanged from the Y chromosome to autosomal or X-chromosome-linked regions.

Discussion

Two Y-chromosome-linked markers (OtY1 and GH-Y) have been found to be predominantly associated with the male sex in natural populations of Chinook salmon from British Columbia, the Yukon, and Washington, Oregon, and Idaho states. Normal sex linkage of each Y-chromosome marker individually (i.e., males possessing and females lacking) was 98.7% for OtY1 and 97.2% for GH-Y, whereas normal linkage for both markers together has been observed in 96.7% of 2478 Chinook salmon examined among 55 populations. In family crosses, cumulative data among studies (Devlin et al. 2001; this study) have indicated that both markers are less than 1 cM from the sex-determination locus, consistent with data from the present population survey, which also indicates a high degree of stability of the Y-chromosome genetic linkage of the markers (but formally does not reflect genetic distance). Indeed, one marker (GH-Y) is Y-chromosome-linked in at least five *Oncorhynchus* species (Devlin et al. 2001; Zhang et al. 2001), indicating that it has remained sex-linked during the radiation of this genus for at least 11 million years (McKay et al. 1996). The other marker, OtY1, is present only on the Y chromosome in Chinook salmon, suggesting that it arose after GH-Y and after the Chinook salmon diverged from its sister-species (coho salmon) at least 6 million years ago.

Exceptions to the strict Y-chromosome linkage or normal molecular structure of GH-Y and OtY1 loci were also discovered in the populations examined. Such exceptions may arise in our sampling because of biological factors such as sex reversal (see below) or molecular differences (sequence variation or deletion) associated with the OtY1 and GH-Y loci, or because of analytical errors such as mislabeling or contamination of field-collected samples or PCR reactions. To minimize the latter errors, we routinely amplified controls lacking template, and samples were reanalyzed from tissue in the rare cases where exceptions were observed. Our use of multiple sex-linked markers serves to minimize errors arising from non-biological variation such as contamination. We were not able to control for contamination or misidentification occurring at the field-collection stage, but the very low frequency of exceptional individuals (males lacking or females possessing both markers) observed suggests that such errors were extremely rare if they occurred at all (see the footnote to Appendix A for possible exceptions). Further, exceptions identified by PCR were in some cases confirmed and found to correlate with changes observed by Southern-blot analysis, which is much less sensitive to contamination errors.

Male Chinook salmon possess significantly ($P < 0.001$, $\chi^2 = 23.09$, 1 df) more variation than females (6.9% and

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Fig. 4. Southern-blot analysis of *Bam*HI-digested DNA from Babine River Chinook salmon, revealing size variation among OtY8 repeats and relationship to the presence and absence of GH-Y strong (+), null (–), and weak (W) alleles. M, testis-containing fish; F, ovary-containing fish.

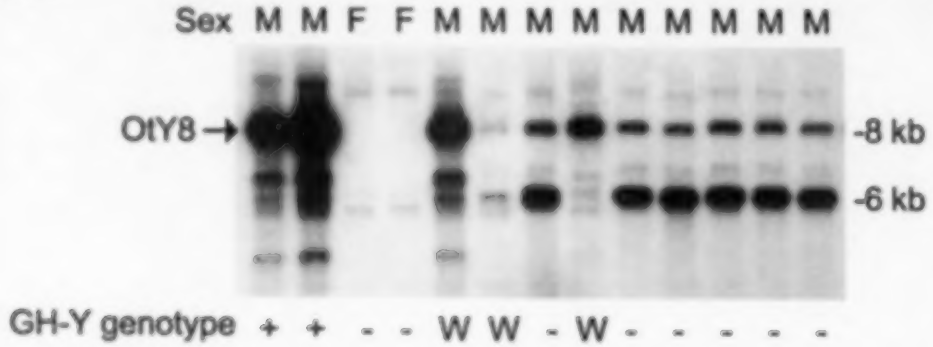
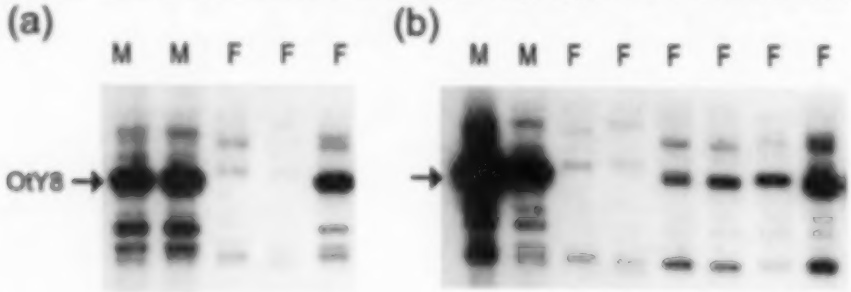


Fig. 5. Southern blots of *Bam*HI-digested DNA from Cowichan River (*a*) and Robertson Creek (*b*) Chinook salmon (M, testis-containing fish; F, ovary-containing fish). In each panel, lanes 1 and 2 are normal males and lanes 3 and 4 are normal females. For Cowichan River, lane 5 contains an exceptional female that was found to possess the OtY1M band by PCR amplification. For Robertson Creek, lanes 5–8 contain females with OtY8 that have the following PCR genotypes: OtY1F, OtY1M, OtY1MF, and OtY1MF.



2.8%, respectively), consisting of both the absence of or weakly amplifying alleles of GH-Y and OtY1. Currently, we do not know the basis for the weak amplification of GH-Y in some individuals, but it could arise from sequence variation around the PCR primer binding sites. The complete absence of GH-Y in males (3.6%) may also arise by sequence variation, as well as by deletion of the GH-Y locus or recombination between this marker and the sex-determination locus on the X and Y chromosomes. If GH-Y is not located between the sex-determination locus and OtY1, then single recombination events could easily yield Y chromosomes lacking the GH-Y marker. The theoretical reciprocal recombinant class (females with GH-Y) was represented more rarely (2.1%) within populations, suggesting that if differential selection of chromosomes is not responsible, deletion rather than recombination is probably responsible for the majority of males lacking GH-Y alleles and that removal of this locus can occur without disruption of the sex-determination locus. For the *O. masou* species complex (masu salmon, amago salmon (*O. m. ishikawae*), Biwa salmon (*O. masou* ssp.), and their hybrid, Honmasu salmon), both classes of exceptions were identified in some populations (Zhang et al. 2001), and thus both recombination and sex reversal were considered possible explanations.

If recombination is responsible for rare exceptions to the Y-chromosome linkage of GH-Y and OtY1 in salmon, then the recombinant chromosomes (i.e., Y chromosomes lacking and X chromosomes possessing GH-Y or OtY1) must be at a selective disadvantage and must be eliminated from populations to allow long-term persistence of Y-chromosome linkage in the majority of individuals, since even very low levels of recombination will usually prevent establishment of sex-specificity of a marker on the sex chromosomes (Charlesworth 1991; Rice 1996). If exchange events between the X and Y chromosomes are unequal and cause deletions or duplications in the sex-limited portion of these chromosomes, such changes may be sufficient to affect chromosome fitness. In some cases, complete elimination of the GH-Y locus in all individuals may have occurred in *Oncorhynchus* species: the amago salmon appears to be negative for GH-Y among all individuals examined (Nakayama et al. 1999; Zhang et al. 2001), and although not definitively demonstrated, sockeye salmon may also not possess a GH-Y locus (Devlin et al. 2001). Sockeye salmon have recently undergone a Y-autosome fusion (Thorgaard 1978; Ueda and Ojima 1984*a*), which may have resulted in the rearrangement or deletion of the GH-Y locus during this translocation event. We have also not detected the presence of GH-Y in rainbow trout and Atlantic salmon (*Salmo salar*), but based on phylogeny analysis, it would be anticipated that GH-Y could be found in rainbow trout, suggesting historical deletion of the locus in this species (Devlin et al. 2001). How-

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ever, caution should be used before concluding that a locus is absent within a species (i.e., Atlantic and sockeye salmon and rainbow trout) until exhaustive analyses of different populations have been undertaken.

For the OtY1 marker, Southern-blot analysis showed that males with weakly amplifying alleles can possess reduced numbers of copies of the OtY8 repeat, suggesting that deletions, unequal recombination, or translocation events are able to alter the structure of this locus. The number of repeat sequence on Y chromosomes is determined by dynamic processes of amplification and deletion that result in a particular copy number at equilibrium (Charlesworth 1994, 1996; Rice 1996). However, by examining large numbers of individuals within a population, one can capture intermediates within this process where some individuals will have recently experienced either an amplification or a deletion event. In humans, exchange events between repeat elements on the Y chromosome have been identified (Schwartz et al. 1998). However, in our studies, few (0.7%) males were completely deficient in OtY1, suggesting that at least some of the OtY8 repeats associated with this marker are genetically quite close to the sex-determination locus. OtY8 repeats are present some 300 times on the Y chromosome, whereas GH-Y is single copy and would be easier to remove by deletion. Complete, or near complete, deletions of OtY8 sequences might often remove the male-determining gene(s) on the Y chromosome and result in female development. Indeed, we have identified rare exceptional females in populations that contain small numbers of OtY8 repeats, consistent with this possibility. The results of the present study indicate that DNA markers in close proximity to the sex-determination locus in Chinook salmon are relatively stable, but there is also variation that could lead to differentiation of sex chromosomes over evolutionary time.

That some variation has been detected among individuals indicates that very strong species-wide selective sweeps (Underhill et al. 1996; Jobling et al. 1998; Filatov et al. 2001) of the Y chromosome are not occurring with high frequency, although such events may well be occurring within individual populations. Indeed, variants were not randomly distributed among all populations, nor equally distributed between US and Canadian populations. Geographic clustering of exceptions would be influenced by the homing nature of Chinook salmon, but suggests that variants can in some cases persist and move between populations by straying of adult fish during their migration at sexual maturity. Some enhanced systems from Washington State (Entiat and Elochoman) with higher frequencies of variant females have experienced historical importation of novel stock and possible bottlenecking. If Y-chromosome-linked sequences (particularly those that are repetitive) apply some negative fitness to the organism, then autosomal or X-chromosome-linked versions of these sequences may be preferentially eliminated from natural populations relative to the frequency seen in enhanced populations.

Recently, a high incidence (84%) of females possessing the OtY1 marker has been identified in wild Chinook salmon from the Hanford Reach region of the Columbia River in Washington State (Nagler et al. 2001). Similar findings have also been reported for Chinook salmon from the San Joaquin River basin in California (Williamson and May 2002), where females possessing the OtY1 marker have been detected at levels up to 38%. These observations differ considerably from those reported in the present study for Chinook salmon from British Columbia, the Yukon, Washington, Oregon, and Idaho, and provide an interesting difference in organization of this locus among geographically distinct populations. It is unclear at this time whether the presence of OtY1 in females in the Hanford Reach and California populations previously described (Nagler et al. 2001; Williamson and May 2002) is due to sex-reversal events arising from external factors (e.g., endocrine disruption or temperature effects) (Craig et al. 1996; Afonso et al. 2002; Azuma et al. 2004), internal factors (the action of autosomal feminizing genes or the creation of a new sex-chromosome pair) (e.g., Komen et al. 1992), or the breakdown of Y-chromosome linkage of the OtY1 marker in this stock (i.e., exchange to the X chromosome or autosomes). Differences in allele-detection technology (agarose versus acryl amide gels, capillary electrophoresis) may also lead to some differences in allele scoring, but are unlikely to cause major differences in frequencies observed among populations. Sex reversal (feminization) of Chinook salmon in laboratory experiments can produce XY females that yield YY progeny in crosses with normal XY males, and these YY males subsequently sire all-male progeny (Devlin et al. 2001). However, we have not observed all-male broods in crosses involving sires collected from the wild in British Columbia (R.H. Devlin, unpublished data), which suggests that YY individuals are rare or absent in nature because they either have low viability or because too few true XY females are present in nature to allow YY progeny to be produced. In the case of California and Washington Chinook salmon previously studied (Nagler et al. 2001; Williamson and May 2002), females possessing strong and weak OtY1 amplification signals were observed at higher frequencies than exceptional females identified in populations in this study. In the present study we have shown that OtY8 repeats can vary in number among males and also can be found rarely in females, and that the majority of these OtY1-positive females are negative for GH-Y. These data indicate that strains possessing OtY1 sequences in females can arise from natural population variation at this locus (and (or) rare exchange or transposition of these sequences from the Y to other chromsomes), rather than from sex reversal, where we would expect both Y-chromosome-linked markers to be present in the exceptional females. Thus, our data indicate that sex reversal is not occurring at high frequencies in the samples of populations we examined. Application of the GH-Y sex-linked marker and a recently described third Y-chromosome marker for Chinook salmon (Brunelli and Thorgaard 2004), as well as testing the progeny of exceptional females, may help reveal whether genetic variation or sex reversal can best explain the presence of OtY1 sequences in the phenotypic females in the Hanford Reach and California samples. It is of interest that the sample of Hanford Reach Chinook salmon analyzed in the present study possessed normal sex-marker genotypes, indicating that sex reversal was not occurring in our samples, an observation that differs from a study of this system previously reported (Nagler et al. 2001). Such marked differences in sex-marker genotypes among studies suggest that events which produce

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such variant fish may be temporally or geographically very limited in their effects. This may have been anticipated, since frequent true sex reversal of XY individuals caused by external factors could have long-term serious implications for a species. Alternatively, rare apparent sex reversal (i.e., where Y-chromosome markers have simply moved to the X chromsome or autosomes and are thus not exclusively associated with the Y chromosome) may well pose no serious threat to Chinook salmon populations.

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Appendix A

Appendix appears on the following page.

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Table A1. Distribution of sex-marker genotypes of male and female Chinook salmon (*Oncorhynchus tshawytscha*) derived from British

Origin	*n*	Gonad	GH-Y+; OtY1M	GH-Y−; OtY1F	GH-Y+; OtY1MF	GH-Y+; OtY1F	GH-Y+; OtY1M
Total (n = 2478)	1139	Testis	1060 (54)	5 (5)	10 (4)	3 (2)	6 (5)
	1339	Ovary	7 (5)	1302 (54)		1 (1)	5 (3)
1. Yukon River	27	Testis	27				
	25	Ovary		25			
2. Babine River	25	Testis	16				1
	25	Ovary	25				
3. Kitsumkalum River	14	Testis	14				
	24	Ovary	24				
4. Kitimat River	49	Testis	38				
	50	Ovary		49			
5. Atnarko River	27	Testis	20		3		1
	25	Ovary		25			
6. Chuckwalla River	12	Testis	6		3		
	19	Ovary		19			
7. Wannock River	19	Testis	19				
	18	Ovary		18			
8. Yakoun River	1	Testis	1				
	23	Ovary		23			
9. Chekamus River	47	Testis	46				
	46	Ovary		46			
10. Marble River	24	Testis	21		2		1
	24	Ovary	.	24			
11. Cousma River	24	Testis	24				
	24	Ovary		24			
12. Robertson Creek	50	Testis	50				
	33	Ovary		28			
13. Sarita River	8	Testis	8				
	8	Ovary		8			
14. Nitinat River	26	Testis	26				
	26	Ovary		26			
15. Quinsam River	25	Testis	25				
	27	Ovary		27			
16. Puntledge River (summer)	24	Testis	24				
	25	Ovary		25			
17. Puntledge River (fall)	24	Testis	24				
	4	Ovary		4			
18. Big Qualicum River	94	Testis	94				
	94	Ovary		94			
19. Little Qualicum River	24	Testis	24				
	24	Ovary		24			
20. Cowichan River	24	Testis	24				
	24	Ovary	1	23			
21. Stave River	24	Testis	24				
	24	Ovary		22			1
22. Harrison River	29	Testis	29				
	29	Ovary		29			
23. Chilliwack River	45	Testis	45				
	46	Ovary		46			
24. Coldwater River	4	Testis	4				
	4	Ovary		4			
25. Spius Creek	11	Testis	10				
	25	Ovary		25			
26. Nicola River	20	Testis	15		2		
	25	Ovary		25			
27. Shuswap River	25	Testis	25				
	25	Ovary		25			
28. Quesnel River	7	Testis	5				
	5	Ovary		5			
29. Dome Creek	41	Testis	39				
	39	Ovary		39			
30. Nechako River	1	Testis					
	6	Ovary		6			

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Columbia, Yukon, Washington, Oregon, and Idaho populations.

GH-Yw; OtY1MF	GH-Yw; OtY1F	GH-Y–; OtY1M	GH-Y–; OtY1MF	Male variation (%)	Female variation (%)	Male exceptions (%)	Female exceptions (%)
19 (4)		28 (11)	8 (2)	6.9 (21)		0.4 (5)	
4 (3)	11 (5)	2 (2)	7 (3)		2.8 (14)		1.2 (10)
2			6	36.0			
11				22.4			
	1				2.0		
3				25.9			
3				50.0			
		1		2.2			
				12.5			
	2	1	2		15.2		
					4.2		4.2
			1		8.3		4.2
		1		9.1			
		1	2	25.0			
		2		28.6			
		2		4.9			
		1		100.0			

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Table A1. (*concluded*)

Origin	*n*	Gonad	GH-Y+; OtY1M	GH-Y−; OtY1F	GH-Y+; OtY1MF	GH-Y+; OtY1F	GH-Yw; OtY1M
31. Salmon River	2	Testis	2				
	0	Ovary					
32. Similkameen River	26	Testis	25				1
	20	Ovary		18			
33. Chewack River	18	Testis	14	1			
	22	Ovary		22			
34. Methow River (spring)	11	Testis	10				
	9	Ovary		9			
35. Methow River (summer)	12	Testis	12				
	24	Ovary		23			
36. Twisp River	12	Testis	12				
	28	Ovary		26			
37. Entiat Hatchery	22	Testis	19				2
	23	Ovary	1	16			
38. Nason Creek	8	Testis	8				
	4	Ovary		3			
39. Wenatchee River	22	Testis	21			1	
	25	Ovary		25			
40. George Adams Hatchery[a]	3	Testis	3				
	9	Ovary		9			
41. White River	11	Testis	8	1[b]			
	13	Ovary	1[b]	12			
42. Elochoman River	15	Testis	14	1			
	31	Ovary	3	21			3
43. Cowlitz River	3	Testis	3				
	11	Ovary		11			
44. E.F. Lewis River	15	Testis	15				
	23	Ovary	1	21		1	
45. Washougal River	16	Testis	14			2	
	31	Ovary		30			1
46. Carson Hatchery	24	Testis	24				
	24	Ovary		24			
47. Clackamas River	1	Testis	1				
	1	Ovary		1			
48. S. Santiam River	1	Testis	1				
	1	Ovary		1			
49. Klickitat River (summer)	8	Testis	8				
	40	Ovary		39			
50. Klickitat River (fall)	6	Testis	6				
	35	Ovary		35			
51. Marion Drain	26	Testis	26				
	10	Ovary		10			
52. Hanford Reach	18	Testis	18				
	18	Ovary		18			
53. W.F. Yankee Creek	25	Testis	11	1			
	20	Ovary		20			
54. Rapid River	49	Testis	49				
	53	Ovary		53			
55. Lemhi River	10	Testis	9	1			
	68	Ovary		68			

Note: GH-Y+, GH-Y marker present; GH-Y−, GH-Y marker absent; GH-Yw, weakly amplifying variant of GH-Y+; OtY1M, normal strong PCR signal of OtY1 male bands with female bands present. Populations are ordered from top to bottom in an approximate north to south arrangement. Numbers all variation detected and the percentage of exceptions indicates either males lacking or females possessing both markers.

[a]Individuals were sampled at age 2.

[b]Labeling error during sampling may have resulted in misassignments of the correct gonadal phenotype between these two fish.

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GH-Yw; OtY1MF	GH-Yw; OtY1F	GH-Y–; OtY1M	GH-Y–; OtY1MF	Male variation (%)	Female variation (%)	Male exceptions (%)	Female exceptions (%)
				3.8			
	1		1		10.0		
		3		22.2		5.6	
		1		9.1			
1					4.2		4.2
2					7.1		7.1
		1		13.6			
	6				30.4		4.4
	1				25		
				4.5			
		2		27.3		9.1	
					7.7		7.7
				6.7		6.7	
		1	3		32.3		19.4
					8.7		4.3
				12.5			
					3.2		3.2
1					2.5		0.3
		13		56.0		4.0	
				10.0		10.0	

for OtY1 male bands present; OtY1F, no detectable amplification of OtY1 male bands (strong amplification of female bands); OtY1MF, weak amplification in parentheses following the summary statistics represent the number of populations in which variants were identified: the percentage of variants includes

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Aggression and feeding of hatchery-reared and naturally reared steelhead (*Oncorhynchus mykiss*) fry in a laboratory flume and a comparison with observations in natural streams

Stephen C. Riley, Christopher P. Tatara, and Julie A. Scheurer

Abstract: We quantified the aggression and feeding of naturally reared steelhead (*Oncorhynchus mykiss*) fry stocked into a laboratory flume with naturally reared fry or hatchery-reared fry from conventional and enriched rearing environments at three densities in the presence and absence of predators, and compared the aggression and feeding observed in the flume to that observed in two streams. Steelhead fry attack rate increased with density and was reduced in the presence of predators, but was not affected by rearing treatment. Threat rate appeared to increase with density and was significantly affected by rearing treatment combination, but was not significantly affected by predator presence. Feeding rate was not affected by density or rearing treatment, but was reduced in the presence of predators. The rate of aggression by steelhead fry in two streams was lower than that observed in the laboratory and did not increase with density. Rates of aggression and feeding of hatchery-reared and wild steelhead fry were not significantly different in the streams. Overall, we found no evidence that hatchery rearing environments caused higher aggression in steelhead fry. Laboratory observations of salmonid aggression, particularly at high density, may not reflect aggression levels in the wild.

Résumé : Nous avons évalué l'agression et l'alimentation d'alevins de truites arc-en-ciel anadromes (*Oncorhynchus mykiss*) élevées en nature et ensemencés dans un canal de laboratoire en présence d'alevins élevés en nature ou en pisciculture dans des environnements ordinaires ou enrichis, à trois densités, avec ou sans prédateurs; nous avons comparé l'agression et l'alimentation observées dans le canal à celles qui existent dans deux cours d'eau. Le taux d'attaque des alevins de truites augmente en fonction de la densité et diminue en présence de prédateurs, mais il est pas affecté par les conditions d'élevage. Le taux de menace semble augmenter en fonction de la densité et est significativement affecté par la combinaison des conditions d'élevage, mais pas significativement par la présence de prédateurs. Le taux d'alimentation n'est pas affecté par la densité, ni par les conditions d'élevage, mais il est réduit en présence de prédateurs. Le taux d'agression des truites dans les deux cours d'eau est plus faible qu'en laboratoire et n'augmente pas avec la densité. Les taux d'agression et d'alimentation des alevins de truite élevées en pisciculture et en nature ne diffèrent pas significativement dans les cours d'eau. Somme toute, il n'il y a pas d'indication que les environnements d'élevage de pisciculture entraînent une plus forte agression chez les alevins de la truite arc-en-ciel anadrome. Les observations d'agression des salmonidés en laboratoire, particulièrement aux densités élevées, peuvent ne pas représenter les niveaux d'agression en nature.

[Traduit par la Réduction]

Introduction

Aggressive interactions among juvenile salmonids are influenced by fish density (Keenleyside and Yamamoto 1962), and may play an important role in salmonid population regulation (Chapman 1966; Elliott 1990; Nakano 1995). A number of studies have indicated that the relationship between aggression and fish density is complex (Sale 1972; Syarifuddin and Kramer 1996; Savino and Kostich 2000). Many studies have suggested that aggression increases with fish density up to a threshold and then decreases with increasing density (Fenderson and Carpenter 1971; Jones 1983; Caballero and Castro-Hdez 2003), although some authors have observed a direct negative relationship between aggression and density (Fleming and Johansen 1984; Brown et al. 1992). Most experiments that have demonstrated a relationship between animal density and aggression have been performed in a laboratory setting, where density is easily

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manipulated. However, there is evidence that animal behavior observed under laboratory conditions may not reflect behavior in the wild (Sloman and Armstrong 2002; Sloman et al. 2002; Wolff 2003).

Animal aggression may also be affected by the presence of potential predators (Lima and Dill 1990). Increased prey activity may increase predation risk by increasing the likelihood of detection by predators (Jakobsson et al. 1995; Martel and Dill 1995), and prey may reduce activity in the presence of predators (Lima and Dill 1990). However, hatchery-reared salmonids may be less likely to reduce activity in the presence of predators (Johnsson and Abrahams 1991), and many laboratory experiments have examined the behavior of juvenile salmonids without the complicating effects of predation.

Supplementation programs that release hatchery-reared fish in an attempt to recover imperiled salmonid populations will result in increases in fish density in streams, which might be expected to affect the social behavior of wild fish. Hatchery-reared salmonids have been observed to be more aggressive than wild conspecifics (Fenderson and Carpenter 1971; Mesa 1991; Sundström et al. 2003), although other studies have reported no difference in aggression (Dickson and MacCrimmon 1982; Weber and Fausch 2003). Because aggressive behavior may be wasteful of time and energy (Bachman 1984) and may increase predation risk (Jakobsson et al. 1995), increased aggression by hatchery-reared fish might be expected to result in negative effects on wild fish in streams where hatchery-reared fish are released, and might negatively affect supplementation efforts for declining salmonid populations (Einum and Fleming 2001). This and other ecological risks associated with the stocking of salmonids for conservation purposes must be understood before supplementation programs can be properly evaluated (ISAB 2003).

Structural modifications to hatchery rearing environments have been proposed as a means of decreasing aggression of hatchery-reared salmonids, but investigations of the effects of structurally enriched rearing on salmonid behavior have produced equivocal results. Significant differences in the aggressive behavior of steelhead (*Oncorhynchus mykiss*) fry reared in conventional and structurally enriched hatchery environments have been observed in some studies (Berejikian et al. 2001) but not in others (Berejikian et al. 2000). The objective of our work was to determine if two types of hatchery-reared steelhead fry were likely to cause increased aggression when stocked with natural fry. We compared the effects of adding steelhead fry reared in conventional or enriched hatchery environments on the aggression and feeding of groups of steelhead fry with the effects of adding equal numbers of naturally reared fry. We attempted to simulate a supplementation release by using fish from the same genetic stock reared under different conditions. To address the potential effects of fish density and predation risk, we quantified feeding and aggressive behavior in laboratory flumes at a range of densities in the presence and absence of yearling conspecifics. We also quantified the aggression and feeding of the same stock of steelhead fry in two streams to compare laboratory results with behavior in natural habitats.

Methods

Rearing treatments

Twenty-five thousand steelhead eggs from artificially spawned hatchery-origin steelhead (16 females and 21 males) from the Skookumchuck River, Washington, were incubated at the Washington Department of Fish and Wildlife's (WDFW) Bingham Creek Hatchery (Satsop River, Washington). The broodstock used to produce hatchery fish for stocking in the Skookumchuck is composed of wild-origin fish captured from the river each year. Eyed embryos were transported to the University of Washington's Big Beef Creek Research Station (Kitsap County, Washington) for final incubation in well water at 10 °C. After emergence, 1667 fry were stocked into each of 12 1.2-m-diameter circular tanks on 12 May 2002. Six conventional tanks contained no cover or structure other than a center standpipe. Six enriched tanks contained the tops of two fir trees to provide structure, military camouflage netting to provide ~60% overhead shade cover, and an underwater food-delivery system to distribute commercial food pellets from automatic feeders through two 2.5-cm-diameter nylon tubes near mid-water depth (four food outlets per tank). Fish in the conventional tanks were fed by automatic feeders that scattered the food across the water surface. All tanks received a constant flow of 40 L·min^{-1} of well water. Fluorescent lights controlled by a 24-h timer mimicked the natural photoperiod.

When emergent fry were stocked into the rearing tanks, 5000 fry were simultaneously released into a screened-off section of a side channel of Big Beef Creek; we refer to these as naturally reared, or natural, fry. The 35-m-long channel received approximately 0.05 m^3·s^{-1} flow from springs and the main channel of Big Beef Creek, and was augmented with 0.025 m^3·s^{-1} well water. The channel had a gravel–cobble substrate and natural early successional riparian vegetation. Woody debris was added to provide structure and cover from predators. Steelhead fry fed entirely on natural food produced within the channel. Steelhead fry in the enriched and conventional treatments were fed with equal frequency and their rations were maintained at a level that kept their growth similar to fry in the channel; mean weights of fry in the three treatments were not significantly different in June ($F_{[2,269]} = 2.25$, $P = 0.1070$, by analysis of variance, ANOVA) or July ($F_{[2,338]} = 1.76$, $P = 0.1734$, by ANOVA).

Laboratory experiment

Experimental facilities

Experimental trials were conducted in two 10 m long × 1.5 m wide flumes previously described by Berejikian et al. (2000, 2001). Flumes were divided down the middle and screens were placed perpendicular to the flow to produce 10 1.5 m × 0.75 m sections in each flume, leaving 2.5 m empty at the downstream end of each flume. The flumes were designed to operate as partially recirculating systems. Water was pumped from a reservoir at the bottom of each flume to a head box at the top of each flume to achieve a flow of approximately 1700 L·min^{-1}. A drain fitted with a standpipe in the lower reservoir maintained the water level at approximately 20 cm and allowed for a constant addition of

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30 L·min^{-1} of well water at 12 °C to maintain water quality. Light was provided by wide-spectrum fluorescent lights over a photoperiod of 14 h light – 10 h dark. All fish were continuously visible to observers through the glass walls of the flumes.

A single-velocity refuge (a 9 cm high × 10 cm wide piece of aluminum) was placed on the substrate (fiberboard) in the center of each flume section 25 cm from the upstream screen. Two custom-made shelters constructed of plastic were placed at an angle against the glass to provide shelter for steelhead fry in each section. The shelters were 61 cm long and were divided into four chambers that fish could enter via 3-cm-diameter holes; fish that used the shelters were visible through the viewing glass.

Experimental protocol

In the lowest density trials, two fry (one natural and one conventional, enriched, or natural fry; total density = 1.8 fry·m^{-2}) were matched for body weight (less than 5% difference) and simultaneously introduced into a flume section; hereafter, these rearing treatment combinations are referred to as CN (conventional and natural), EN (enriched and natural), and NN (natural only). Four (two natural and two conventional, enriched, or natural fry; total density = 3.6 fry·m^{-2}) or eight (four natural and four conventional, enriched, or natural fry; total density = 7.1 fry·m^{-2}) fry were similarly matched for body weight and stocked for higher density trials. One hatchery-reared yearling steelhead from the same stock (mean length = 212 mm, with a range of 175–245 mm) was simultaneously stocked into half of the sections (all sections in one flume; the flume receiving predators was alternated weekly) on each observation date to serve as a predator. Fish were allowed to acclimate in the flume sections for ~44 h and were fed approximately one chironomid larvae each on three occasions daily.

After acclimation, the total number of food items captured and the total number of attacks (nips, charges, and chases) and threats (lateral and frontal displays) initiated by each fish type (natural or hatchery-reared) were recorded simultaneously in each flume section for 10 min by three observers. One chironomid larva per fish was introduced into each section at the onset of observation and every two min thereafter (a total of five larvae per fry) during observation periods. The larvae entered each section through a polyvinyl chloride (PVC) tube that was located in the center of the section at the upstream end and positioned at a 45° angle to the left such that fish that positioned themselves in the upstream-most position on the left side of the section had first access to food.

Fry used in this experiment ranged from 42 to 91 mm in length and from 0.68 to 6.94 g in weight; fish size increased over the duration of the experiment, but experimental factors were balanced over time. Yearling steelhead consumed fry on only four occasions; these trials were not considered in the analysis and were repeated to ensure a balanced design. It was not necessary to mark steelhead fry because fry from the three rearing treatments differed in color and fin quality. Although differences were not quantified, fry from both hatchery-rearing treatments had a strong bluish hue (the rearing tanks were blue) and eroded fins, and were easily distinguishable from naturally reared fry by trained observers.

The order of observation was from downstream to upstream in each flume, and treatments and densities were balanced among flumes, flume sections, and observation dates. All observations took place between 0800 and 1300 Pacific Standard Time. Water temperature in the flumes ranged from 13 to 16 °C during observations. A total of 180 trials (10 replicates of three rearing treatment combinations at three densities in the presence and absence of yearling steelhead) were observed between 11 July and 26 September 2002.

Field observations

Field sites

Field observations were conducted in Eleven and Twelve creeks, two second-order tributaries of the upper Skookumchuck River in the Chehalis River drainage in southwestern Washington. Fish passage to the upper Skookumchuck is blocked by Skookumchuck Dam, but WDFW transports several hundred adult steelhead above the reservoir each spring to spawn naturally. In addition to steelhead, cutthroat trout (*Oncorhynchus clarki*) and sculpins (*Cottus* spp.) are present in Eleven and Twelve creeks.

Eleven and Twelve creeks are dominated by cobble–gravel substrate and drain natural second-growth riparian forest. A single study reach on each stream was bounded by a weir on the downstream end and a natural barrier to migration on the upstream end. The lengths of the study reaches were 483 and 560 m on Eleven and Twelve creeks, respectively, and mean wetted widths were 5.2 and 5.5 m, respectively. Each reach was divided by a weir into two sections of approximately equal length. Weirs were constructed of panels (0.6 m × 1.5 m) framed with PVC pipe and covered in 6-mm wire mesh. Panels were attached to steel fence posts driven into the stream banks and substrate.

Fish stocking

Four thousand hatchery-reared steelhead fry were stocked into Eleven and Twelve creeks on 13 August 2002; 1000 fish of a single rearing treatment (enriched or conventional) were stocked into each section. Hatchery-reared fish were double marked with adipose and pelvic fin clips (to distinguish them from wild fish) and were released at the midpoint of each study section. Steelhead reared in enriched environments were stocked into the upstream section of Twelve Creek and the downstream section of Eleven Creek; conventionally reared steelhead were stocked in the downstream section of Twelve Creek and the upstream section of Eleven Creek. An additional 250 hatchery steelhead of the same rearing treatment were introduced into each section on 27 August 2002. These fry were given combinations of adipose and pelvic fin clips to distinguish them from the previously stocked hatchery steelhead and were also stocked at the midpoint of each section. Fish from the second stocking were not distinguishable from the earlier stocked fish during snorkel surveys. Steelhead fry dispersed quickly and were found throughout the study reaches within a week after release.

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Table 1. ANOVA results for comparisons of attack rate, threat rate, and feeding rate of steelhead (*Oncorhynchus mykiss*) fry in a laboratory flume. Rearing treatment combinations used in this experiment were naturally reared steelhead fry combined with equal numbers of fry reared in a natural, conventional hatchery, or enriched hatchery environment.

	Model	Treatment combination	Density	Predator	T×D	T×P	D×P	T×D×P
df	17, 162	2, 162	2, 162	1, 162	4, 162	2, 162	2, 162	4, 162
Attacks	**0.0001**	0.7686	**0.0001**	**0.0001**	0.3663	0.5066	0.5827	0.5732
Threats	**0.0001**	**0.0351**	**0.0001**	0.7377	0.6972	0.5994	0.0679	0.3174
Feeds	**0.0001**	0.6088	0.2795	**0.0001**	0.2819	0.8733	0.4988	0.1074

Note: T×D, treatment combination by density interaction; T×P, treatment combination by predator interaction; D×P, density by predator interaction; T×D×P, three-way interaction. Values shown are significance levels (P) of ANOVA tests. Significant values appear in boldface. df, degrees of freedom.

Observations

Frequencies of feeding and aggression were estimated for wild and hatchery fish by underwater observation in Eleven and Twelve creeks. Divers entered each study section from downstream and moved upstream slowly to minimize fish disturbance. When a group of two or more fry was encountered, the diver counted the number of fry of each rearing group (wild or hatchery-reared) within an area of 0.5 m^2. Divers observed all fry within this area and recorded the number of aggressive acts and feeding strikes by hatchery and wild fry during a 5-min period. Feeding strikes included both attempts and successful strikes; aggressive acts included all types of threats and attacks because it was not practical for divers to record threats and attacks separately. Data were recorded underwater on plastic slates. Behavioral observations were collected on five occasions between 20 August and 10 September 2002. Because cutthroat trout fry are difficult to distinguish from steelhead fry by snorkeling, some of the wild fish that we observed may have been cutthroat. Stream temperature ranged from 10 to 15 °C during observations.

Data analysis

Laboratory data

We used a substitutive design (Fausch 1998) to compare the effects of adding fry reared in conventional or enriched hatchery environments on the aggression and feeding of groups of steelhead fry with the effects of adding equal numbers of naturally reared fry. Data were analyzed using a balanced factorial three-way ANOVA design with rearing treatment combination, density, and predator (yearling) presence as factors. We tested the hypothesis that the rates of threats, attacks, and feeding were not different among the three rearing treatment combinations, among the three densities, or in the presence or absence of predators. Data were log-transformed before analysis. We did not include fish size as a covariate in this analysis because there was no significant relationship between the numbers of attacks, threats, or feeding strikes observed and the mean length or weight of steelhead fry (in all cases $P > 0.1$, $R^2 < 0.015$, by linear regression).

Field data

Because field observations were not balanced across streams, sampling dates, and rearing treatments, we did not attempt analyses to determine if differences in feeding or aggression existed between streams, rearing treatments, or among sampling dates. Rather, we calculated the mean number of aggressive acts (attacks plus threats) and feeding attempts for wild and hatchery-reared (enriched and conventional combined) steelhead fry in Eleven and Twelve creeks at local densities ranging from 4 to 11 fry·m^{-2} and compared these data with that collected in the flumes. Sample sizes for observations of feeding and aggression ranged from 7 to 60 groups of fish at each density.

Results

Laboratory experiment

Attacks

We observed significant effects of density and predator presence on the number of attacks per fish, but no effect of rearing treatment combination was evident (Table 1). The rate of attacks by steelhead fry tended to increase with density; the single exception to this was the CN treatment in the presence of predators (Fig. 1*a*). In the presence of predators, steelhead fry reduced the number of attacks that they initiated (Fig. 1*a*). In most cases, the 95% confidence limits for the rearing treatment combinations overlapped (Fig. 1*a*), suggesting that differences among treatment combinations were not significant.

Threats

We observed significant effects of rearing-treatment combination and density on threat rate (Table 1). The number of threats per fish generally increased with fish density (Fig. 1*b*). Unlike attack rate, the rate of threats was not always reduced in the presence of predators, and there was no significant effect of predator presence on threats (Table 1). Differences in threat rate among treatment combinations were more apparent than for attack rate, particularly in the absence of predators and at high density. The NN treatment combination exhibited the highest threat rate at all densities when predators were present, and at the lowest and highest densities when predators were absent.

Feeding

We observed a significant effect of predator presence on feeding rate; no other main effects or interactions were significant for this variable (Table 1). The feeding rate of steelhead fry appeared to remain stable across densities, but was reduced in the presence of predators (Fig. 1*c*). Differences among rearing treatment combinations, although not significant, were more apparent in the presence of predators.

Total aggression and feeding in the field and flumes

Rates of total aggression (threats and attacks combined) by hatchery-reared and wild steelhead fry in Eleven and

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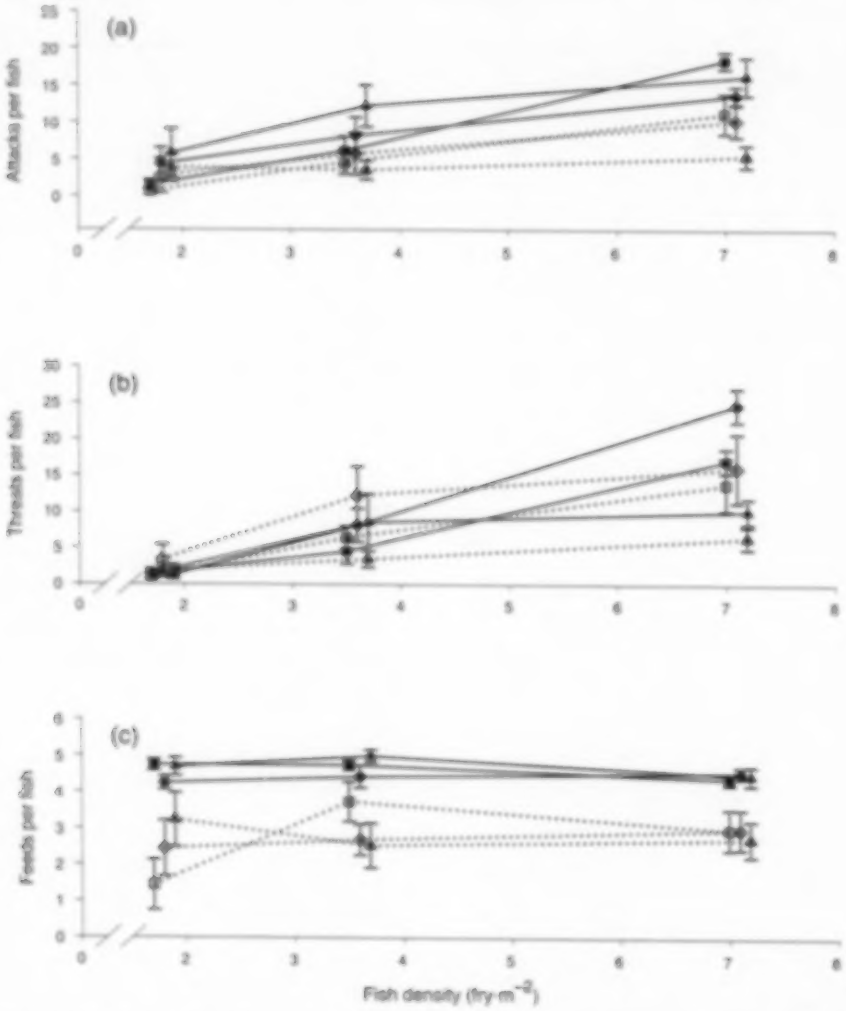
Fig. 1. The number of (*a*) attacks, (*b*) threats, and (*c*) successful feeding attempts observed per fish for three rearing combinations of steelhead (*Oncorhynchus mykiss*) fry at three densities in the presence and absence of yearling steelhead parr in experimental flumes. Error bars are 95% confidence limits. Rearing treatment combinations used in this experiment were naturally reared steelhead fry combined with equal numbers of fry reared in a natural (NN, diamond symbols), conventional hatchery (CN, triangle symbols), or enriched hatchery (EN, square symbols) environment. Treatments were observed in the presence (broken lines with open symbols) and absence (solid lines with solid symbols) of potential predators (yearling steelhead). Symbols are slightly offset on the *x* axis to allow confidence intervals to be distinguished.



Twelve creeks were generally lower than those observed in the flume experiment and showed no increase with fish density (Fig. 2*a*). Total aggression (threats and attacks) by natural steelhead fry in the laboratory was greater than that of hatchery fry at all densities in the presence and absence of predators (Fig. 2*a*). There was no significant difference in aggression rate between hatchery-reared and wild fry in the streams over the range of densities examined ($F_{[1,358]} = 0.03$, $P = 0.8607$, by ANOVA).

Feeding rates of wild and hatchery-reared fry in Eleven and Twelve creeks were variable, similar to those observed in the flume, and showed little change with density (Fig. 2*b*). The feeding rate of hatchery-reared steelhead fry in the laboratory was higher than that of natural fish in the absence of predators at the two lowest densities, while the feeding rate in the presence of predators was higher for hatchery-reared fish at the two highest densities (Fig. 2*b*). Feeding rates of hatchery-reared and wild steelhead fry in Eleven and Twelve creeks differed at higher densities (Fig. 2*b*), but there was no consistent pattern. Averaged across densities, the feeding rate of hatchery-reared fry in the streams was not significantly different than wild fry ($F_{[1,358]} = 2.87$, $P = 0.091$, by ANOVA).

Discussion

Previous work has provided equivocal evidence regarding the effects of rearing environment on the aggressive behavior

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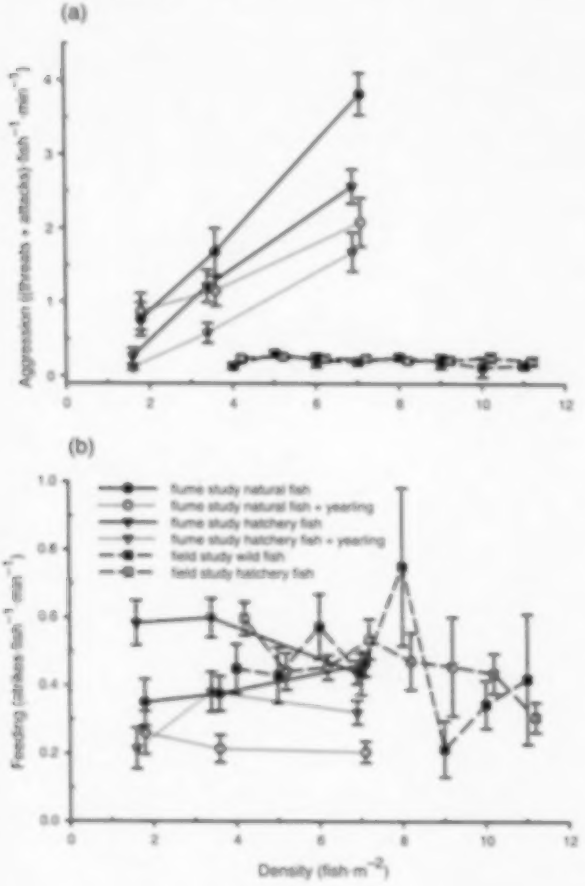
Fig. 2. The mean number of (*a*) aggressive acts (attacks and threats) and (*b*) feeding strikes by steelhead (*Oncorhynchus mykiss*) fry over a range of local densities in laboratory flumes and two natural streams. Error bars are 95% confidence limits. Where error bars are not visible they are obscured by the symbols. Hatchery fry include fish reared in both conventional and enriched hatchery environments. Symbols are slightly offset on the *x* axis to allow confidence intervals to be distinguished.



of steelhead fry (Berejikian et al. 2000, 2001). Berejikian et al. (2000) observed no significant difference in the aggressive behavior of steelhead fry reared in conventional and enriched hatchery environments when the treatments were stocked together at 10.7 fry·m^{-2}. However, when naturally reared steelhead fry were stocked with both hatchery treatments at a lower density (5.3 fry·m^{-2}), there were significant differences among rearing treatments in the frequency of threat displays by dominant fish (conventionally reared fry delivered significantly fewer displays than enriched or natural fry) but not of attacks (Berejikian et al. 2001). When fry from each of the three rearing treatments were observed separately at a density of 4.0 fry·m^{-2}, Berejikian et al. (2001) observed a significant difference in the relationship between body size and total aggression among the three treatments: aggressiveness increased with body size in the enriched and conventional hatchery treatments, but not in naturally reared fry. In the present study, rearing treatment combination appeared to affect the rate of threats but not the rate of attacks by groups of steelhead fry in the laboratory. Groups of naturally reared fish initiated more threats than groups that included fish reared in conventional or enriched hatchery environments in some cases, but threat rate was not consistently lowest for either mixed (EN or CN) rearing treatment combination across densities. These results indicate that the mixed groups of naturally reared and hatchery-reared steelhead fry do not exhibit higher levels of aggression when compared with naturally reared fry under laboratory conditions. Moreover, it appears that the relative aggressiveness of groups containing conventional or enriched fry is dependent on density and predation risk. The differences between the results of the present work and those of Berejikian et al. (2000, 2001) highlight the importance of estimating aggression levels over a range of densities.

Previous studies have suggested that environmental differences associated with hatchery rearing resulted in increased aggression in juvenile salmonids (Einum and Fleming 2001). Although animal aggression may have consequences for population dynamics (Huntingford and Turner 1987; Nakano 1995; Mougeot et al. 2003), the potential consequences of increased aggression by hatchery fish on wild salmonid population dynamics are unclear. It has been suggested that increased aggression might result in higher mortality of hatchery-reared fish due to lost feeding time, high energy use, and increased risk of predation. However, other factors besides aggression may be important in the population regulation of stream salmonids, and the most aggressive or dominant fish may not be the most successful (Hojesjo et al. 2002). We found little evidence that hatchery rearing environments caused increased aggression in steelhead fry in the laboratory or in the streams, suggesting that the aggression-related impacts of supplementation stocking of steelhead fry on wild steelhead fry, at least at moderate densities, may be minimal.

It is important to note that our study addresses potential differences in aggression and feeding that are caused by rearing environment, since the fry used were from the same genetic stock. However, it is possible that selection on the rearing treatments may have differed because naturally reared fry were subject to predation, while the hatchery-reared fry were not. We removed most potential fish predators from the channel before stocking fry, but naturally reared fry were likely to have been exposed to predation by belted kingfishers (*Ceryle alcyon*) and mink (*Mustela vison*) during rearing. Further research is necessary to determine the relative roles of physical rearing environment and differential predation mortality on the behavior of naturally reared steelhead fry.

We observed significant effects of fish density on steelhead fry aggression in the laboratory, with the numbers of attacks and threats per fish generally increasing as density increased. Increases in the level of aggression with density have been previously observed in juvenile salmonids (Fenderson and Carpenter 1971; Keeley 2000) and other fish species (Jones 1983) in laboratory or culture settings, although other studies indicate that aggression increased up to intermediate densities and then decreased (Fenderson and Carpenter 1971; Cole and Noakes 1980; Caballero and Castro-Hdez 2003), and some have observed no difference

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or reduced aggression at high densities (Fleming and Johansen 1984; Brown et al. 1992; Hedenskog et al. 2002).

Resource defense theory predicts that individuals should defend a resource if the benefits of defense exceed the costs (Grant 1993, 1997). Therefore, the aggression rate exhibited by an individual should be related to population density and the characteristics (e.g., amount, distribution in time and space) of the resource that is being defended (Grant 1997). Numerous studies have demonstrated that fish aggression is affected by the abundance and distribution of food resources (Slaney and Northcote 1974; Ryer and Olla 1996; Grant et al. 2002), and the discrepancies among studies of the relationship between fish density and aggression might be at least partly due to different food levels used in the experiments. In the present study, food abundance per fish was constant among density treatments, and the results represent density-related changes in aggression that are not confounded by food abundance.

There were no significant effects of density on the mean number of successful feeding attempts by steelhead fry in the laboratory. This result was expected because, as noted above, the amount of food per fish was held constant across densities. Because we enumerated only successful feeding strikes, these data do not represent total feeding activity, which might be expected to change with density (Johnsson 2003).

The presence of yearling steelhead significantly reduced feeding by steelhead fry in the laboratory experiment. A number of authors have reported that salmonid feeding is reduced in the presence of potential predators or predator models (Metcalfe et al. 1987; Dionne and Dodson 2002; Johnsson 2003), although some studies have found no effect or an increase in feeding in the presence of predators (Martel 1996; Reinhardt and Healey 1997). The effects of predator presence on fish behavior may depend on prey species (Magnhagen 1988), fish size (Reinhardt and Healey 1999; Dionne and Dodson 2002), habitat (Holiethoek and Power 1995; Reinhardt and Healey 1997), and prey hunger level (Gotceitas and Godin 1991). We observed no consistent differences among rearing treatment combinations in feeding in the presence of predators, suggesting that mixed groups of natural and hatchery-reared steelhead fry are unlikely to differ from groups of natural fry in their feeding response to the presence of a potential predator.

We observed a significant reduction in the number of attacks, but not threats, by steelhead fry in the laboratory when predators (yearling steelhead) were present. It has been suggested that potential prey may tend to reduce activity when predators are present to minimize the risk of detection (Metcalfe et al. 1987). Several studies have reported a decrease in aggressive behavior by salmonids in the presence of predators (Martel 1996; Martel and Dill 1993; Reinhardt 1999), although this may depend on the abundance and distribution of food (Ryer and Olla 1996; Vehanen 2003). The fact that the threat rate was not reduced in the presence of potential predators may be related to reduced vigilance of potential prey that might be associated with attacks but not with threats (e.g., Jakobsson et al. 1995). Because predators are probably rarely absent from habitats where wild salmonids occur, including predators in laboratory experiments may make results more realistic (but see below).

Steelhead fry released into Eleven and Twelve creeks generally exhibited lower aggression than that found in the laboratory and did not show an increase in aggression with density over a similar range of densities to that which we observed in the laboratory. Although we are unaware of other studies that have examined density–aggression relationships of steelhead fry in streams, Chapman (1962) similarly did not observe an increase in aggressive behavior (nips per min) of juvenile coho salmon with density (ranging from 2 to 7 fish·m^{-2}) in an Oregon stream. Grant (1990) and Keeley and Grant (1995) reported low frequencies of aggression (0.13 and 0.135 mean aggressive acts·fish^{-1}·min^{-1}, respectively) for wild juvenile salmonids in streams that are within the range observed for steelhead fry in Eleven and Twelve creeks.

Aggression in groups of fish has been shown to decrease with increasing food abundance (Slaney and Northcote 1974; Gregory and Wood 1999; Grant et al. 2002). Fish distribution in streams may be related to food abundance (Power 1984; Kawaguchi et al. 2002), and denser groups of salmonids may tend to be found in areas with higher rates of drifting food (Elliott 2002). Therefore, it is possible that denser groups of fry observed in Eleven and Twelve creeks had congregated in areas with higher drift rates. The fact that we did not observe a reduction in feeding strikes per fish as density increased in the streams may indicate that groups of steelhead fry were positioned in areas with drift rates proportional to group size. In our laboratory experiment, the level of food delivered matched fish density (particles per fish per minute), and feeding rates were similar in the flume and in the field. To put this another way, aggression rates in the wild may be ameliorated by emigration: subordinate fish may emigrate from areas where aggression levels are too high (Chapman 1962; Mason and Chapman 1965; Nakano 1995), and this may serve to regulate aggression. The fact that fish were confined within the flume sections in the laboratory may have caused increased aggression by preventing emigration.

There are several reasons why our field results may have differed from those in the laboratory. Wild fry that were observed in the field would have enjoyed prior residence, which may give juvenile salmonids an advantage in foraging and territorial disputes (Deverill et al. 1999; O'Connor et al. 2000; Metcalfe et al. 2003), while hatchery-reared and naturally reared fry in the flume were introduced simultaneously. The presence of a diver may also have affected fry behavior in the streams, although divers were careful to observe only fish that did not visibly react to their presence. The simple nature of the flume habitat may also have affected aggression; Mork et al. (1999) noted that aggression by juvenile Atlantic salmon (*Salmo salar*) was higher over a simple fiberglass substrate than over a cobble substrate, and Basquill and Grant (1998) reported that aggression by zebrafish (*Danio rerio*) was reduced in more complex habitats.

Water quality and other physical characteristics of the flume environment may also have affected aggression levels in the laboratory. Griffiths and Armstrong (2000) found that aggression initiated by juvenile Atlantic salmon toward non-kin conspecifics was higher when water was recirculated than when it was not. Our experiment was con-

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ducted with recirculated water, and this may have affected aggression. The water temperature range was slightly higher in the flumes than in the stream, which may also have affected aggression levels.

We are aware of no other studies that have explicitly compared salmonid aggression levels in field and laboratory situations. Because our field results suggest that aggression levels are mostly lower than those observed in the flume, even at the lowest density tested, it may be necessary to use lower densities in laboratory experiments of salmonid aggression to obtain results that are applicable to fish in the wild. Many laboratory studies of salmonid aggression have used very high densities (Keenleyside and Yamamoto 1962, 2.6–72.3 fish·m^{-2}; Fenderson et al. 1968, 21.4 fish·m^{-2}; McNicol and Noakes 1984, 24–60 fish·m^{-2}; Keeley 2000, 32–127 fish·m^{-2}; Hedenskog et al. 2002, 9.6–159 fish·m^{-2}), and the relevance of measurements of aggression at such high densities to many field situations may be questionable. Further research is necessary to determine the appropriate density at which to conduct laboratory experiments of salmonid aggression.

In summary, our laboratory results suggest that levels of aggression in mixed groups of hatchery-reared and naturally reared steelhead fry were not consistently higher than in groups of naturally reared fry, and that aggression generally increased with fry density and decreased in the presence of potential predators. Our laboratory results also suggest that aggression should be observed over a range of densities before drawing conclusions about the relative levels of aggression exhibited by different rearing types. Our field observations suggest that there was little difference in the rate of aggression between wild and hatchery-reared steelhead fry in natural streams, and that aggression rates observed under laboratory conditions may be much higher than observed in streams. Moreover, we did not observe an increase in aggression with fry density in the field. This work demonstrates the importance of validating behavioral observations made under laboratory conditions with field observations.

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Foraging of royal albatrosses, *Diomedea epomophora*, from the Otago Peninsula and its relationships to fisheries

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Abstract: Foraging zones used by incubating royal albatrosses (*Diomedea epomophora*) from the Otago Peninsula and their coincidence with fisheries activities were studied with global positioning system (GPS) loggers. Birds favoured areas around the shelf break of the eastern New Zealand continental mass, with hot spots of activity that coincided with fishing zones actively exploited by commercial trawl fisheries during the study period. Birds appeared to change their behaviours with proximity to fishing events, showing reduced speed and more direct flight when at moderate distances from fishing operations (12.5–25 km) than at greater distances. This relationship was significant for speed only ($P < 0.029$). Fishing operations for hoki (*Macruronus novaezelandiae*) and deep-sea species were those with the most numerous associations with royal albatross foraging flights and were also the most common during the study period. Waters along shelf breaks within 100 km of the breeding colony were extremely important for royal albatrosses, 28% of GPS locations being obtained within this radius from the Otago Peninsula study. Royal albatrosses from Campbell Island, studied previously, had also fed in this area extensively. Birds spent 2–19 days at sea, travelling 2000 km, on average, during their foraging trips.

Résumé : Des enregistreurs GPS (système de positionnement global) ont permis de déterminer les zones de recherche de nourriture des albatros royaux (*Diomedea epomophora*) de la péninsule d'Otago et leur recoupement avec les zones d'activité de pêche. Les oiseaux préfèrent les régions avoisinantes de la bordure orientale du plateau continental de la Nouvelle-Zélande, avec des points de forte utilisation qui coïncident avec les zones de pêche activement exploitées par le chalutage commercial durant la période d'étude. Les oiseaux semblent changer leur comportement à proximité des activités de pêche commerciale : ils réduisent leur vitesse et volent plus directement lorsqu'ils sont à des distances moyennes (12,5–25 km) des opérations de pêche que lorsqu'ils en sont plus éloignés. Cette relation n'est statistiquement significative que dans le cas de la vitesse ($P < 0,029$). Les opérations de pêche du hoki (*Macruronus novaezelandiae*) et des espèces de haute-mer sont celles qui sont le plus associées aux vols de recherche de nourriture de l'albatros royal; ce sont aussi celles qui ont été les plus communes durant la période d'étude. Les eaux limitrophes de la bordure du plateau situées à moins de 100 km de la colonie reproductive ont une grande importance pour l'albatros et contiennentt 28 % des signalisations GPS dans ce rayon dans notre étude dans la péninsule d'Otago. Les albatros de l'île Campbell, étudiés précédemment, se nourrissent aussi abondamment dans cette région. Les oiseaux passent 2–19 jours en mer et couvrent une distance moyenne de 2000 km au cours de leurs sorties de recherche de nourriture.

[Traduit par la Rédaction]

Introduction

Royal albatrosses (*Diomedea epomophora*), like other members of the order Procellariiformes, spend up to 95% of their lives at sea (Weimerskirch and Wilson 2000), with long interbreeding migrations throughout the southeastern Pacific Ocean and southern Atlantic Ocean (Robertson and Kinsky 1972; Nicholls et al. 2002). During these periods away from the nest, they are vulnerable to injury or mortality through marine pollution and interactions with fishing operations

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(Murray et al. 1993; Klaer and Polacheck 1995; Reid and Sullivan 2004). Royal albatrosses have been recorded killed in trawl operations targeting a variety of midwater and deep-sea species, and in longline fishing for tuna in the New Zealand region (Table 1; Murray et al. 1993; Bartle 1991; Robertson et al. 2003).

Albatrosses and petrels may also draw considerable food resources from associating with fishing vessels (Thompson and Riddy 1995; Freeman and Smith 1998; James and Stahl 2000). They are known to scavenge baits during the setting and hauling of longline gear, and to feed from offal and fish rejected during fish-processing aboard vessels. For long-lived species such as albatrosses, defining the extent of these "beneficial" and "detrimental" effects in population terms is complex. However, to appreciate the factors operating in the marine environment that may affect a particular population's well-being, study of individuals' foraging movements during the different parts of the annual cycle is necessary (Monaghan 1996).

At meso- to macro-scales in the oceanic environment (scales of 100–1000 km), fish abundance or marine productivity can explain seabird densities, while at finer scales, such relationships are difficult to detect (Abrams 1985; Hunt 1990, 1991). The complex nested patches of productivity in marine systems can be explained by a hierarchical patch structure (Wu and Loucks 1995). Foraging patterns of wandering albatrosses (*Diomedea exulans*) show that they may be exploiting such complex environments (Viswanathan et al. 1996), and seabird densities in relation to those of their prey fish have been explained using this model (Fauchald 1999; Fauchald et al. 2000). These authors showed how murres (*Uria* spp.) foraging on capelin (*Mallotus villosus*) tracked large- to medium-scale patches of prey. At the smallest scales identified (<3 km), however, these relationships could not be detected. Similar findings were made for least auklets (*Aethia pusilla*) in relation to plankton biomass (Hunt et al. 1990).

Fauchald et al. (2000) predicted that when tracking prey patches up such a hierarchical system, predators would show increased rates of turning and alighting on the surface as they move towards smaller and denser prey patches. Birds may also use other top predators' behaviours as a guide to rich feeding areas (Harrison et al. 1991; Fauchald et al. 2000). Aside from physical oceanographic processes and resulting prey assemblages, a major feature thought to elicit responses in bird foraging patterns is the presence of vessels, particularly during fishing operations (Hudson and Furness 1989; Petyt 1995). However, few studies have demonstrated a functional relationship between fishing operations and seabird behaviour.

In this study we examined trawl-fishing activity as a variable in the foraging environment exploited by royal albatrosses using global positioning system (GPS) loggers to determine whether regional to mesoscale coincidence of zones of exploitation by fisheries and birds was occurring within the New Zealand Exclusive Economic Zone (NZEEZ). At a finer scaled resolution we investigated whether the birds' behaviour showed any response to the proximity of fishing activities. We hypothesize that seabirds searching for exploitable productive patches in regional-scale foraging areas will coincide with fisheries in their distribution. Further, where fishing activity influences seabird foraging behaviour, we predict measurable behavioural responses in seabirds. Here we tested flight speed and an index of sinuosity of flight (work index) in response to the proximity of fishing events.

We aimed to use a preliminary data set of 18 albatrosses' foraging trips to examine the nature and extent of any interactions between foraging seabirds and fishing activities, using catch-effort data and bird behavioural data. From this basis, we make recommendations intended to allow more targeted gathering of information on any adverse effects of fishing on royal albatrosses from our study population.

Methods

Northern royal albatrosses, *Diomedea epomophora sanfordi*, nesting at Taiaroa Head were studied from 5 to 31 December 2002 (hereinafter the study period). Each bird was fitted with a GPS logger for one trip only. Twenty birds were studied, from which 18 complete tracks were obtained. For the remaining two birds, the retrieved loggers did not contain data, but the birds continued their breeding activities normally.

GPS BGDL-II+ loggers were used, set to record data at 1-h intervals, as described by Fukuda et al. (2004). The location interval was designed to allow coverage of whole trips, given uncertainty about foraging-trip duration for the study population. The loggers weighed 67 g and had an estimated accuracy of the positional fixes of 10 m, with 95% of all locations falling within this range when the birds remained stationary on their nests (Fukuda et al. 2004). Loggers were attached by adhesive tape and cable ties to the back feathers of birds while they were incubating. Birds were not restrained during attachment. Of the successful deployments, 10 males and 7 females were followed, and 1 bird was of unknown sex. All birds had bred at least once prior to the study season.

Fishing-event data

Data on fishing events undertaken by New Zealand fisheries were obtained from the New Zealand Ministry of Fisheries Catch Effort database *Warehou* (Ministry of Fisheries 2002). Fishing events used in the analysis were those that occurred during the study period and within a zone encompassed by the maximum extent of the royal albatrosses' foraging locations (hereinafter the study zone). An event was defined as the setting or hauling in of the fishing net. Events were excluded from the analysis when the time of the event (in hours and minutes) and (or) the location was not recorded. The data set retained for analysis represented 3649 trawl shots of a total of 4466 possible events recorded in the study zone and period (82%). For spatial analysis, set and haul locations were treated separately. Fishing data with adequate information came from trawl fisheries targeting 16 fish stocks (Table 1). Data for longline fishing events were excluded because sample sizes were small ($n = 6$ sets for tunas) and timing data and haul location were not recorded for bottom longline sets targeting ling, *Genypterus blacodes* ($n = 84$ sets). Further, as some fisheries active in the study zone used more than one fishing method, and not all location parameters are required to be reported for some operations

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Table 1. Fishing events used in the analysis, by target fish species, with royal albatross (*Diomedea epomophora*) mortalities observed in New Zealand trawl-fishing operations.

Fishery	Scientific name	No. of fishing events used	Proportion of events used by target-species fishery	Percentage of total events in study area/period	No. of royal albatross mortalities[a]
Barracouta	*Thyrsites atun*	238	1	6.5	1
Alfonsino	*Beryx splendens*	32	0.58	0.9	
Cardinal fish	*Epigonus telescopus*	14	1	0.4	
Hake	*Merluccius australis*	64	1	1.8	
Hoki	*Macruronus novaezelandiae*	1402	1	38.4	3
Ling	*Genypterus blacodes*	138	0.83	3.8	1
Oreo	*Pseudocyttus maculates, Allocyttus niger*	340	1	9.3	
Orange roughy	*Hoplostethus atlanticus*	368	1	10.1	1
Red cod	*Pseudophycis bachus*	43	0.37	1.2	
Scampi	*Metanephrops challengeri*	615	1	16.9	1
Gemfish	*Rexea solandri*	15	1	0.4	
Sea perch	*Helicolenus* sp.	138	1	3.8	
Arrow squid	*Nototodarus sloanii, Nototodarus gouldi*	172	0.99	4.7	3
Silver warehou	*Seriolella punctata*	15	1	0.4	
Tarakihi	*Nemadactylus macropterus*	36	0.22	1.0	
Blue warehou	*Seriolella brama*	19	0.44	0.5	
Total		3649	0.84[b]		10

[a]Ministry of Fisheries unpublished data for 2000–2002 (Chief Scientist, Ministry of Fisheries, P.O. Box 1020, Wellington, New Zealand); includes mortalities of both northern and southern royal albatrosses.
[b]Average.

(e.g., for smaller vessels and some inshore fisheries), only a proportion of fishing events were used for these fisheries in the analyses (Table 1; the average proportion of events used was 84%; range 22%–100%).

These catch-effort data were sourced from fishers' returned logbooks and may contain some errors or inaccuracies. Locations of trawl shots and hauls were recorded to 1′ of longitude and latitude and to 1- or 5-min time intervals, depending on the fishery. Error in the data is not quantifiable and is assumed to be unbiased. To avoid assumptions concerning rounding methods used by fishers when recording vessel locations, an error of 1 naut. mi. is assumed for all location measures. It is assumed that all fishers had GPS navigation equipment and could obtain equally accurate positional fixes at sea.

Study species and site

Royal albatrosses breed exclusively in New Zealand, and there are two geographically separated subspecies: the northern royal albatross breeds at Taiaroa Head on the Otago Peninsula (25 pairs) and at the Chatham Islands (2500 pairs), while the southern royal albatross, *Diomedea epomophora epomophora*, breeds on the Campbell and Auckland islands (8000 pairs) (Barrie and Robertson 1996).

Bird data

GPS data were edited to remove locations at the colony, and time of departure and arrival was estimated as the time at which the last (or first) colony-based location reading was recorded at the beginning and end of a visit to sea, respectively. Sex differences in average trip duration, maximum distance from the colony, and distance travelled were examined. No significant differences were found, so data were pooled ($z = |0.2 - 0.8|$; $z_{critical} = 1.9$ for two-tailed test with a difference of 0, not significant (ns)).

The 18 bird trips were run in *Diomedea* custom software (D. Filippi, unpublished software) to estimate additional parameters on bird movement: (*i*) cumulative distance — the total distance travelled by a bird that would be measured by taking a route joining successive GPS locations; (*ii*) vectorial distance — the distance travelled by a bird in a direct line from the beginning to the end of a given period, here 6 h; (*iii*) work index — cumulative distance minus vectorial distance over a 6-h period, following Gremillet et al. (2000), further developed by Waugh and Weimerskirch (2003); (*iv*) distance travelled during the trip (km); (*v*) maximum distance from the colony (km); (*f*) speed of travel between two locations ($km \cdot h^{-1}$); and (*vi*) distance between GPS locations and fishing events (set or haul) occurring within 30 min of a bird's passage through a given point (km).

In addition to calculating each of these parameters at the interval of the GPS location, *Diomedea* estimates the position of birds and associated parameters at 1-min time intervals between locations, assuming a constant speed of displacement and direction of travel. From these estimated positions, a matrix of bird activity was generated by summing data on bird travel times into cells of 1′ of latitude and longitude. This matrix was used to describe the density of bird activity by unit area, in bird-hours, cumulatively for the study period over the whole study area. The units of this density matrix are expressed in bird-hours per unit area. Owing to differences in the numbers of birds in this and previous studies (Waugh et al. 2002; Waugh and Weimerskirch 2003), these indices should be considered relative only within a particular study. Here we choose to graphically represent bird density in categories of 150 and 400 bird-hours per 1′ of longitude and latitude.

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Previous research on movements of royal albatrosses using satellite tracking and activity recorders has shown that this taxon is equally active in prey-searching behaviours (take-offs and landings, movements and circuitous flight) at night and during the day, with peaks of activity around dawn and dusk (Waugh and Weimerskirch 2003). For this reason we consider that royal albatrosses can forage at any time in a 24-h period. Further, birds tended to show high rates of landing and take-off around periods when the work index was high, although there was no significant statistical correlation between these indices, owing to the large scatter of data at low values for both indices. For southern royal albatrosses, at the height of feeding activity at dawn and dusk, the work index peaked at 70 for 80% of the birds in the sample (n = 10) and showed average values of 7.2 (±2.1) (Waugh and Weimerskirch 2003; H. Weimerskirch and S. Waugh, unpublished data).

Seabird mortality data were sourced from observer records for the period 1994–2002 and include all royal albatrosses reported killed in trawl fisheries in the New Zealand zone during this period (Chief Scientist, Ministry of Fisheries, P.O. Box 1020, Wellington, New Zealand, unpublished data). All captures were reported from the period 2000–2002.

Bird – fishing event interactions

A matrix of fishing-event locations over 1′ longitude and latitude cells was generated and integrated with that of bird density, giving a new matrix that showed bird densities in cells where fishing events occurred. It should be noted that fishing events occurred extensively throughout the study zone, and were not restricted to those areas where albatrosses foraged. These are not represented graphically, owing to data sensitivity. "Kernels" of density are smoothed in the plots to form the most parsimonious polygons from the data.

We estimated the distance in kilometres between a bird at a given hourly location and the nearest fishing event that occurred within a half-hour period of the bird's GPS locational fix. A half-hour period was chosen to limit the distance vessels could have travelled from the recorded fishing location. Error can enter into this interaction-distance estimation in a number of ways: firstly, vessels may have moved during the interval between the fishing event starting and the bird's location being recorded (a maximum of 30 min); secondly, fishing-event locations are recorded to the nearest nautical minute (equivalent to 1.852 km for degrees of latitude) in fishers' logbooks, and assuming no bias in the recording of fishing locations, event data could be assumed to have an error of this distance, which, conservatively, would need to be doubled to avoid assumptions about the rounding of part-degrees by different operators; lastly, error in recording bird locations using GPS exists, but this was considered to be negligible. Vessel speeds recorded at the time of the fishing event varied between 0 and 7.1 kn, with the vessel-displacement error estimated at 3.86 ± 0.73 kn (mean ± SD). Vessel speeds over 20 kn were assumed to be erroneous and were excluded (n = 7). Using an assumed vessel speed of 4 kn during gear setting or hauling, the maximum distance of travel was estimated within a 30-min period from the recorded time of the fishing event. We therefore assume that the average precision with which we can assign fishing event – bird locations is 9.0 km, which is the sum of these errors.

To test whether birds' behaviour changed with proximity to fishing events, we tested differences in the work index and speed of individual birds that were and were not in proximity to fishing events. For this analysis, only GPS locations were used for 16 birds for which fishing events occurred within the 1-h window of opportunity. To determine which fishing operations for target-fish species were occurring in proximity to bird tracks, we summed the minutes of time that birds spent within 25 km and 30 min for each of the 16 different target-stock trawl fisheries in our data set.

Statistical methods

Values are reported as means ± SD unless stated otherwise. Work index, speed, and distance to fishing location were log-transformed to normalize their distributions. A general linear model procedure was used to test response variables (work index, speed) to variation in distance to fishing events, with individual bird as a categorical variable. Analyses were carried out in Statistica™ 6.0 (StatSoft 2001). We investigated a modelling approach to comparing spatial coincidence of fishing activity and bird density, but rejected this approach, as the current data set for birds was too small and 1-h spacing of GPS locations precluded a finer scaled analysis. Therefore, the work remains a preliminary examination of the comparison of fishing- and bird-activity data, albeit at a coarse level.

Results

Description of foraging trips

Birds spent an average of 8.2 days at sea, travelling 2081 km, the average maximum distance from the colony being 529 km (Table 2). Trips divided into local and long-distance trips, with a strong relationship between distance travelled and trip duration (r^2 = 0.88, n = 18). The areas most frequented were the waters from the Otago Peninsula along the eastern New Zealand shelf break to the Mernoo Bank (Fig. 1). Outside of the Otago Peninsula area, localized areas of intensive usage occurred around the western edge of the Chatham Rise (Mernoo Bank) and midway along the northern edge of the Chatham Rise at around 180°E.

Trips restricted to the waters off the Otago Peninsula (n = 4) were of less than 4 days in duration and birds stayed within 100 km of the colony. All birds visited an area of shelf break between the Otago Peninsula and approximately the 45°S parallel of latitude, and 28% of GPS locations were recorded within this area (Figs. 2 and 3). For the remainder of the trips (5–19 days, n = 14), birds travelled extensively around the eastern edge of the New Zealand shelf from south of the New Zealand mainland to the east coast of southern North Island (Table 2; Fig. 1). Thirteen of the 18 birds frequented the Mernoo Bank area during their trips, and 6 spent extensive periods over the Chatham Rise. Two birds visited the waters off the Kaikoura Peninsula.

Interaction with fishing events

We plotted the density of bird activity in the cells where fishing events also occurred during the study period (Fig. 4). Fishing density was not explored graphically, owing to sensitivity of the data on fishing locations and catch effort. This plot indicates that the central foraging areas used by north-

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Table 2. Specifications of 18 royal albatross foraging trips tracked with GPS loggers from the Otago Peninsula, including foraging-trip durations, travel distances and destinations, the number of fishing events occurring within 25 km of the bird's track, and 30-min intervals of passage.

Bird ID No.	Sex	Duration of foraging trip (days)	Distance travelled during trip (km)	Maximum distance from colony (km)	No. of fishing events at <25 km	Mean travel speed ($km \cdot h^{-1}$)	No. of GPS locations recorded during trip	Location of foraging trip
82	M	2.2	465	130	1	8.90	46	Otago Peninsula only
74	F	3.2	457	93	0	6.44	54	Otago Peninsula only
70	F	3.8	578	112	4	4.38	79	Otago Peninsula only
87	F	4	915	101	1	10.66	75	Otago Peninsula only
77	M	5.2	1292	299	0	12.77	84	Otago Peninsula, Mernoo Bank
71	M	6.1	1868	440	3	12.37	142	Otago Peninsula, Mernoo Bank
83	M	6.2	698	233	0	nd	40	Canterbury Bight, southeast South Island
80	M	6.4	2682	856	4	18.04	143	Mernoo Bank, Chatham Rise
84	F	6.9	2545	884	0	nd	142	North Island east coast of Kaikoura Peninsula
75	M	8.5	4110	1186	5	18.20	158	Chatham Rise, Bounty Island
59	M	9.2	2392	842	3	16.53	76	Chatham Rise
69	F	9.3	2724	828	7	14.45	158	North Island east coast of Chatham Rise
61	M	10.3	1737	345	4	6.75	234	Mernoo Bank
62	Unknown	10.7	2359	380	2	12.39	167	Mernoo Bank
78	M	10.8	3024	509	2	16.90	132	Mernoo Bank, Kaikoura Peninsula
72	M	12.7	4427	1205	4	14.61	228	Mernoo Bank, Chatham Rise
73	F	12.9	901	337	0	6.23	27	Canterbury Bight
88	F	19.3	4293	755	7	9.79	363	Mernoo Bank, Kaikoura Peninsula, Chatham Rise
Mean		8.2	2081	529		11.82	130	
SD		4.2	1317	368		4.46	84	

Note: M, male; F, female; nd, no data.

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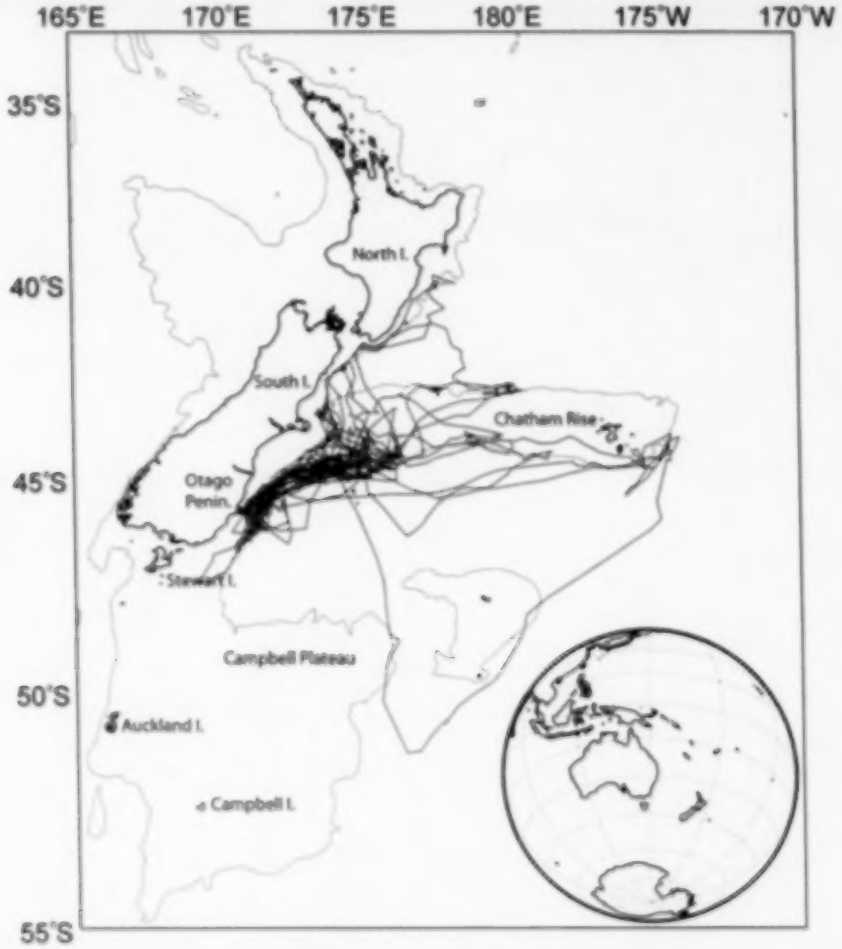
Fig. 1. Tracks (thin solid lines) of 18 royal albatrosses (*Diomedea epomophora*) followed using GPS loggers (BDGL II+) from the Otago Peninsula in December 2002. The dotted line indicates the 1000-m contour and the thick solid line indicates the coast.



ern royal albatrosses, along the eastern shelf break from 48 to 40°S, coincided with actively used fishing areas for the study period. The areas used most intensively by the albatrosses coincidentally with fishing within the study zone were the Mernoo Bank and the northern Chatham Rise. These are also the locations where 10 royal albatross mortalities had been recorded by fisheries observers during 2000–2002 (Fig. 4).

Individual bird tracks relative to fishing events

At a finer scale we examined the track of each bird to determine whether it passed in proximity to fishing events occurring within 30 min of its passage through a certain point. Representative tracks from birds 59, 70, and 71 are plotted (Figs. 2, 5, and 6).

Bird 70 moved along the shelf break to the south of the Otago Peninsula, where several fishing events occurred in proximity to its flight track (Fig. 2). The close spacing of the hourly location points in proximity to the two discrete areas of fishing activity indicate that the bird's travel was slow through these areas compared with the remainder of its flight. This bird retraced its path along the shelf break before returning to its nest.

The track of bird 59 moved to the southern Mernoo Bank area, and on to forage extensively on the northern side of the Chatham Rise (Fig. 5). In this area, the bird encountered multiple fishing events within 25 km of its flight track. The zigzagging of the bird's track in the region of the three discrete groups of fishing events suggests prolonged and extensive searching for food in these areas. This bird returned to its nest by retracing its passage along the edge of the Continental Shelf break.

Bird 71 showed a similar pattern to bird 59, but remained on the Mernoo Bank area during a complex zigzagging flight (Fig. 6). This bird foraged in the proximity of four fishing locations near to 44°S, with slow flight in proximity to the fishing events.

Of the remaining birds, five did not encounter fishing events within 25 km of their hourly positional locations, while the remainder each showed a mix of feeding in "hot

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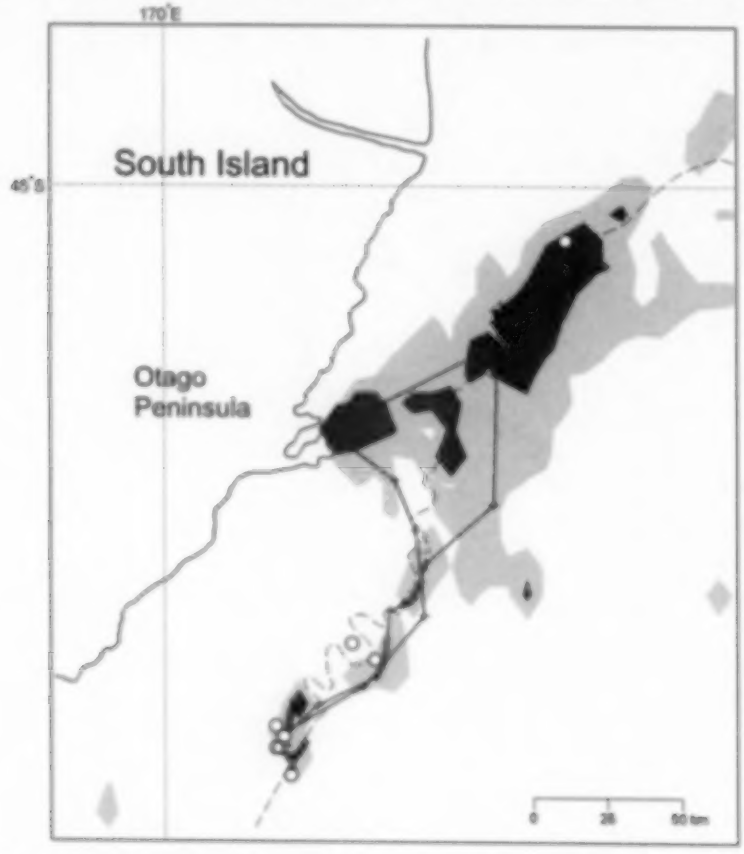
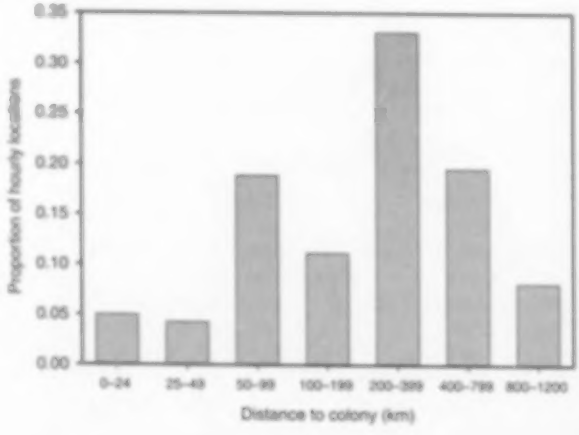
Fig. 2. Density of all birds in the study shown in detail for the Otago coast area, with bird density contours of 150 h (light shaded) and 400 h (dark shaded) per 1′ of latitude by longitude. The track of bird 70 during a 4-day foraging trip is superimposed, with crosses denoting hourly bird positional fixes; open circles indicate trawl-fishing locations occurring within 20 km and 30 min of the bird's track through a location. The broken line indicates the 1000-m contour and the solid line denotes the coast.



spots" in the absence of detectable fishing locations and in areas in close proximity to fishing events (Table 2).

The cumulative time spent by all study birds, in relation to vessels targeting different fish species, where fishing events occurred within 25 km and 30 min of a bird's passage through locations was calculated (Table 3). These data suggest that for these events with close spatial coincidence, trawlers fishing for hoki (*Macruronus novaezelandiae*) represented the greatest risk (41% of time was spent in this distance category), along with those targeting orange roughy (*Hoplostethus atlanticus*) and oreos (*Pseudocyttus maculatus* and *Allocyttus niger*, 41% of time, pooled for these closely associated deep-sea fisheries). The remainder of events were split between a variety of deep-water (e.g., cardinal fish (*Epigonus telescopus*)) and more predominantly inshore fisheries (e.g., gemfish (*Rexea solandri*), barracouta (*Thyrsites atun*), and red cod (*Pseudophycis bachus*)).

Fig. 3. Proportions of bird locations at different distances from the breeding colony.



Behavioural responses to proximity of fishing events

When the behavioural indices of travel speed and work index were examined in relation to proximity to a fishing event, speed showed a significant response, with "bird" explaining a significant component of the variation, while for work index neither bird nor work index explained a significant portion of the variation (Tables 4 and 5). Plotting average speed and work index against distance from a fish-

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Fig. 4. Density of all birds' usage in cells where fishing activity occurred during the study period, showing time spent cumulatively for 18 birds, with density contours of 150 h (light shaded) and 400 h (dark shaded) per 1′ of latitude by longitude. The broken line indicates the 1000-m contour and the solid line denotes the coast. The open circles show the locations of royal albatross mortalities during the period 2000–2002 (n = 10).

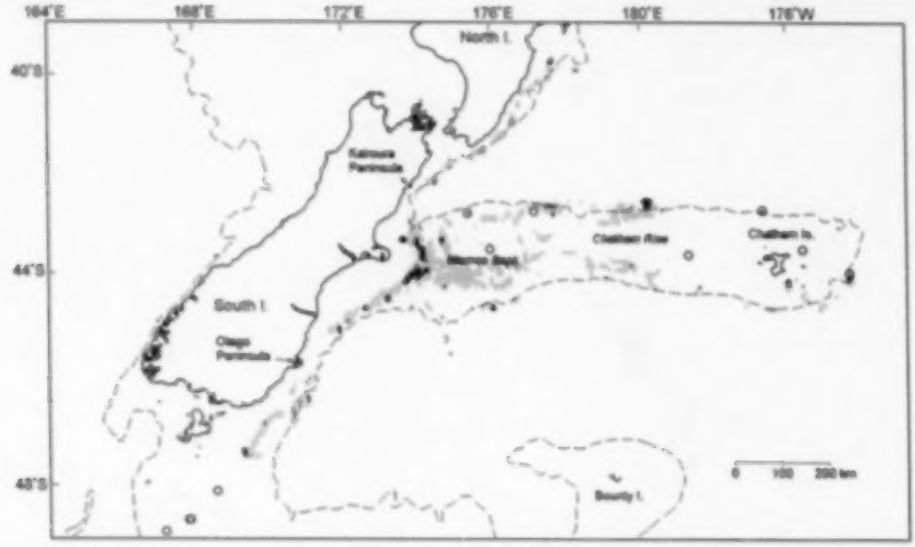
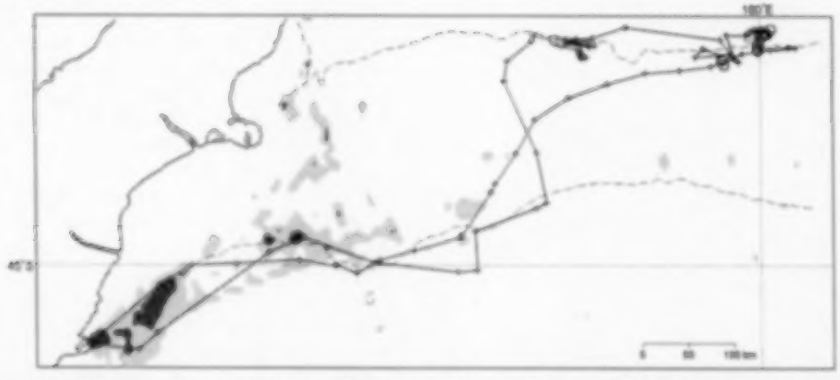


Fig. 5. The track of bird 59 foraging during 9 days. Extensive foraging with low-speed travel is indicated by the sinuous flight path and closely spaced locations around a cluster of fishing locations on the northern Chatham Rise. The density of all 18 birds' usage with density contours of 150 h (light shaded) and 400 h (dark shaded) per 1′ of latitude by longitude is shown. The broken line indicates the 1000-m contour and the solid line denotes the coast. The open circles represent fishing events occurring within 30 min and 25 km of the bird's flight through a point.



ing event shows that the differences in the indices relate to decreases at the 12.5–25 km distance (Fig. 7). At the closest distance plotted (0–12.5 km), the indices of speed and work index showed an increase.

Discussion

Foraging zones used

The northern royal albatrosses tracked during this study used a foraging pattern similar to that of two birds from the same site studied in 1993 (Nicholls et al. 1994), and to that of southern royal albatrosses studied at Campbell Island (Waugh et al. 2002). This was characterized by extensive foraging along shelf breaks and over shelf areas. Dietary studies using regurgitates at nests also showed that the birds fed mainly on shelf-dwelling species of squid (Imber 1999). The Otago Peninsula birds concentrated in particular areas over the shelf break off the Otago Peninsula, Mernoo Bank, and Chatham Rise. These were the hot spots of activity also exploited most heavily by birds from Campbell Island when foraging in northern regions. The extent of the Otago Peninsula birds' foraging was more limited than that of the southern subspecies, which also extensively used areas over the more southerly Snares Shelf and Campbell Plateau during incubation. In explaining these differences, the limited sampling period in the current study, and interannual variations in foraging patterns, cannot be ruled out.

For the conservation of the population studied and mitigation of risks during foraging at sea, the waters within 100 km of the breeding colony are particularly important,

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Fig. 6. The track of bird 71 during a 5-day foraging trip to the western Chatham Rise. The density of all birds' usage in cells is indicated, showing time spent cumulatively for 18 birds, with density contours of 150 h (light shaded) and 400 h (dark shaded) per 1′ of latitude by longitude. The broken line indicates the 1000-m contour and the solid line denotes the coast. The open circles represent fishing events occurring within 30 min and 25 km of the bird's flight through a point. This bird spent extensive periods foraging in an area where four fishing events occurred.

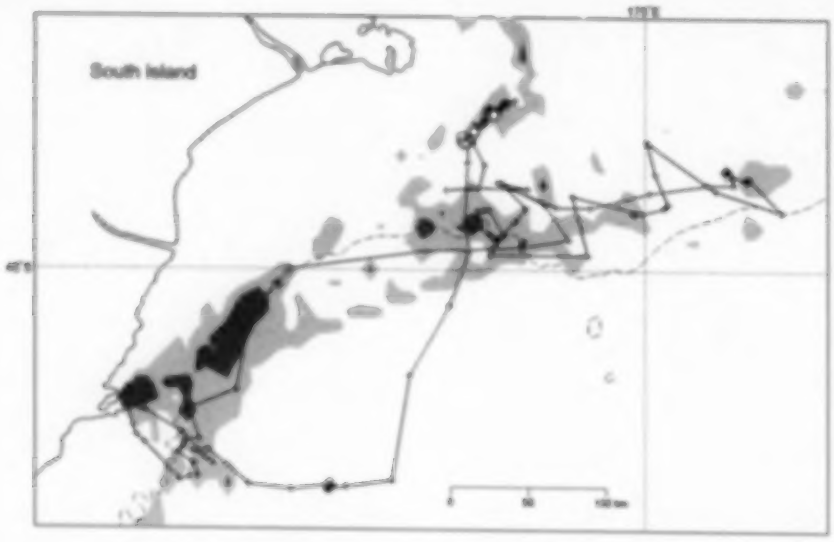

Table 3. Number of minutes spent by 18 royal albatrosses at a distance of less than 25 km and within 30 min of a fishing

Target-species fishery	No. of bird-minutes	Percentage of total bird time
Barracouta	20	1
Black oreo	179	5
Cardinal fish	67	2
Hoki	1456	41
Orange roughy	951	27
Red cod	275	8
Scampi	105	3
Gemfish	60	2
Squid	140	4
Smooth oreo	314	9

because during the study period this area contained over one-quarter of the bird locations recorded, roughly equating to 25% of the time spent at sea by all birds. This zone was also frequented by royal albatrosses from Campbell Island (Waugh et al. 2002), thus providing an important conservation region for the royal albatross. Data on foraging zones of the larger population of royal albatrosses at Chatham Island, gathered during similar stages of the breeding cycle, are currently unavailable, therefore the findings cannot be generalized across the taxon. The Otago Peninsula colony of royal albatrosses has a high public profile because of its proximity to centres of human population and the opportunity this lends to advance awareness of seabird conservation issues. This tiny population is closely monitored, and 3 of the 50 adults that bred in 2004 disappeared during the breeding season, leading to speculation about causes of mortality. In addition to waters off the Otago Peninsula, areas on which attention could be focused to examine risks from fishing activity are along the Mernoo Bank – Chatham Rise. These are the areas in which fisheries observers have recorded mortalities of royal albatrosses.

Most birds from the Otago Peninsula divided their activities between areas with and without detectable fishing activity. Those birds that fed without association with recorded fishing events mainly did so over the shelf waters off the Otago Peninsula, within 100 km of the breeding site. It is important to note that because of fishing regulations, many vessels fishing in these inshore waters are not required to record the latitude and longitude of fishing sets, hence data for the large finfish fisheries operating in this area were inaccessible.

Patterns of behaviour recorded for wandering albatrosses indicate that individuals commonly alternate short feeding spells (<4 days in this case) with more extensive foraging farther from the nest (Weimerskirch 1995; Weimerskirch et al. 1997). It would appear that the feeding strategies of royal albatrosses similarly include undertaking short and long foraging trips.

Changes of behaviour in proximity to vessels

There was a tendency for bird's behaviour to change with proximity to fishing operations. Birds showed increases in speed and work index as they came nearer to fishing events at a scale of 100s to 10s of kilometres. A considerable decrease in both of these indices was observed at the scale of 25–12.5 km, while at the closest distances (<12.5 km), speed and work index again increased.

The patterns of behaviour described by these two indices, considered in tandem, suggest that within the region with active fishing operations (<100 km), birds are actively search-

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Table 4. GLM results for speed in relation to distance from a fishing event.

Speed	Sum of squares	df	Mean squared error	*F*	P
Intercept	0.784	1	0.784	2.577	0.11
Log distance from fishing event	1.474	1	1.474	4.844	0.029
Bird	20.126	15	1.341	4.406	<0.001
Error	49.323	162	0.304		

Table 5. GLM results for work index in relation to distance from a fishing event.

Work index	Sum of squares	df	Mean squared error	*F*	*P*
Intercept	0.339	1	0.339	0.69	0.407
Log distance from fishing event	0	1	0	0	0.993
Bird	9.161	15	0.61	1.242	0.245
Error	77.664	158	0.491		

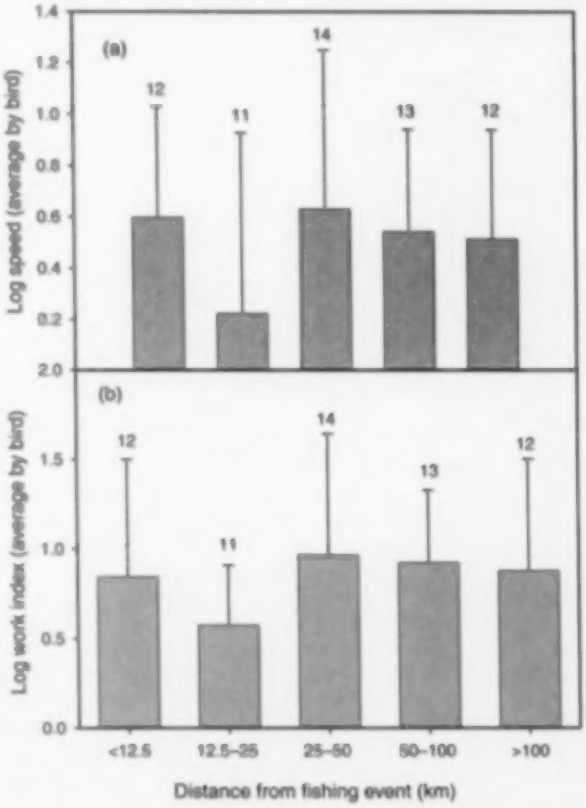
ing for food, using high-speed flight and high turning rates. As birds increased their proximity to fishing events occurring within a short temporal window of their passage (12.5–25 km, half an hour), they adopted low-speed but more direct flight. We speculate that this was due to the use of flapping flight, which is energetically expensive, and relatively low speed rather than soaring flight using wind currents (Weimerskirch et al. 2000). An explanation may be that birds detect vessel operations over these distances and use flapping flight to go directly towards the fishing event. Over distances of less than 25 km, birds may become aware of vessels either by cuing on other birds' behaviours or through the noise or olfactory cues provided by fishing activity. The resolution of the data used in this research does not allow an examination of behaviours at scales finer than 10 km, but the significant relationships shown for speed indicate a relationship between vessel proximity and bird behaviour that merits further examination with higher resolution data.

These findings are consistent with the model, put forward by Fauchald et al. (2000), of hierarchically structured prey assemblages in the marine environment. They suggested that birds' turning rate and landing/take-off rate should increase as they track increasingly dense prey patches. At greatest proximity to the densest, small-scale prey patches, relationships between bird density and prey density dissipated, owing to problems of measuring associated events, which were short-lived and very localized.

The zones used by birds from the Otago Peninsula were also used for fishing operations; they are recognised as productive patches in the NZEEZ (McClatchie et al. 1997) and are heavily exploited by a range of fisheries (Annala et al. 2003). This could be either because birds are responding to the same factors that lead to higher densities of fish biomass which become exploitable for fisheries, or because birds are actively associating with fishing operations. With a larger data set of bird activity and locations captured at shorter time intervals (e.g., 1 min), and increased precision of vessel-location data (such as through GPS data recorded by Vessel Monitoring Systems), it may be possible to examine these relationships statistically in future studies.

When we examined which vessels birds encountered during foraging flights, vessels from the hoki fishery were predominant, followed by deep-sea fisheries for orange roughy and oreos. Birds also foraged in proximity to a range of other fisheries, some of which are considered to be predominantly inshore fisheries (e.g., barracouta, gemfish, red cod). It may be that birds associated with fishing vessels in relation to the frequency of occurrence of vessels fishing for dif-

Fig. 7. Average bird activity indices of (*a*) speed ($km \cdot h^{-1}$) and (*b*) work index (difference between direct and observed connection between successive satellite fixes) for 18 royal albatrosses. Average values and standard deviations are shown for birds in each category of distance from fishing operations. The numbers above the bars refer to the number of birds in the sample for each category.



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ferent target species. Our data do not allow us to test this hypothesis, as we felt that the data set was too limited to describe the "observed" and "expected" distributions of albatrosses in relation to factors in the environment, or the probability of occurrence of vessels. However, in terms of assessing risk for royal albatrosses posed by fishing operations, the study demonstrates that future efforts should be placed in observing the nature and extent of interactions between royal albatrosses with a few fishing fleets, some of which operate in spatially discrete areas.

Feeding associations between vessels and birds may be beneficial for some albatrosses, i.e., when they are successful in obtaining food from trawl operations, and detrimental for others, which are incidentally killed during fishing activities. Royal albatross mortalities recorded in the NZEEZ by observers in trawl fisheries during 2000–2002 have been limited to those target-species fisheries with which birds in this study associated during their foraging flights. The one exception to this is the trawl fishery for ling, with no ling-fishing vessels "visited" by study birds. However, this fishery made up only a small proportion of the total fishing events studied (<4%). Bottom longlining is the most prevalent method used for ling fishing in this area of the NZEEZ (Annala et al. 2003), but this data set was excluded from the present analysis because of the deficiencies of the spatial information recorded for longline fishing for ling, although events were recorded in accordance with current fishing regulations. Further, it should be noted that observer coverage has not been even across fisheries in the New Zealand area, therefore conclusions as to the relative risk posed by each fishery to the albatross species, in terms of mortality, cannot be drawn from these observer data. Trawl fisheries present a risk at an individual level for royal albatrosses, as mortalities have been noted in these fisheries, though during the 1990s many of these mortalities were due to the use of net-sonde monitor cables (Bartle 1991). Birds are clearly closely coincident in time and space with several major trawl fisheries, and mortalities of this species had been recorded in these fishery locations, which are most favoured by foraging royal albatrosses, since the prohibition of net-sonde monitor cables. Further examination of the relationship between spatial coincidence of vessels and foraging birds and the population effects of any mortality of the species is merited.

In conclusion, this study has indicated that concentrated feeding by royal albatrosses along shelf breaks is common to the Otago Peninsula and Campbell Island populations, the same areas being used by both populations throughout the eastern New Zealand continental shelf break during incubation. The marine areas of most consequence for royal albatrosses from the Otago Peninsula occur within 100 km of the breeding site, but localized areas along the continental shelf break are also vital for the food supply for this population. Important feeding locations outside this area occur around the Mernoo Bank, Chatham Rise, and Kaikoura Peninsula. A range of commercial fishing fleets, some of which are visited at close proximity by foraging royal albatrosses from the Otago Peninsula, also use these areas. The hoki and deep-sea fisheries are those for which most coincidents between fishing activity and royal albatrosses' foraging were recorded during the study. The research investigation leads us to conclude that to examine fine-scaled interactions between foraging seabirds and fishing operations, data at the finest possible scale are required. Using GPS data from vessels, and shorter time intervals between locational fixes for bird activity data, along with an increased sample of birds studied, would allow future research to develop modelling approaches to examine vessel–bird associations and make a quantitative assessment of risk to birds from different fishing fleets. When considered at a coarser scale, the present work provides information to allow environmental-resource managers to target their research when attempting to identify the risks faced by individual animals foraging in the marine environment.

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PERSPECTIVE / PERSPECTIVE

Is pelagic top-down control in lakes augmented by benthic energy pathways?

M. Jake Vander Zanden, Timothy E. Essington, and Yvonne Vadeboncoeur

Abstract: Modern food web studies are typically conducted from a trophic dynamic perspective that focuses on combined roles of top-down and bottom-up forces in regulating food web structure. Recognition of spatial food web subsidies in diverse ecosystems highlights the importance of energy flow as a foundation for understanding trophic dynamics. Here, we consider how different energy flow configurations might affect trophic dynamics in north-temperate lakes. A literature review revealed that littoral piscivores exert top-down control on prey fishes. In contrast, analysis of littoral predator diets indicated extensive omnivory and heavy reliance on zoobenthic prey. We explored this uncoupling between trophic dynamics (piscivores regulate prey fish) and energy flow (zoobenthos in piscivore diets) using a biomass dynamic model. This model compared top-down impacts of a piscivore on prey fishes under two scenarios: consumption of prey fish only and consumption of prey fish plus zoobenthos. The model predicted that elimination of zoobenthivory leads to a 50% reduction in piscivore standing stock and concomitant 2.5-fold increase in prey fish abundance (i.e., zoobenthivory plays a key role in mediating pelagic top-down control). These results highlight the role of benthic–pelagic linkages in regulating trophic dynamics and underscore the value of whole-ecosystem approaches to the study of food webs.

Résumé : Les études modernes des réseaux alimentaires sont menées généralement dans une perspective trophodynamique qui se concentre sur les rôles combinés des forces descendantes et ascendantes dans la régulation de la structure du réseau. La reconnaissance des apports spatiaux dans les réseaux alimentaires des différents écosystèmes met en relief l'importance du flux énergétique comme base de la compréhension de la trophodynamique. Nous examinons ici comment différentes configurations du flux énergétique peuvent affecter la trophodynamique dans les lacs tempérés nordiques. Une revue de la littérature montre que les piscivores littoraux exercent un contrôle descendant sur les poissons proies. En revanche, l'analyse des régimes alimentaires des prédateurs littoraux indique une importante omnivorie et une forte dépendance des proies zoobenthiques. Nous avons analysé cette dissociation entre la trophodynamique (les piscivores contrôlent les poissons proies) et le flux d'énergie (le zoobenthos dans le régime alimentaire des piscivores) à l'aide d'un modèle dynamique de biomasse. Le modèle compare les impacts descendants d'un piscivore sur les poissons proies selon deux scénarios, la consommation de poissons proies seuls et la consommation à la fois de poissons proies et de zoobenthos. Le modèle prédit que l'élimination de la consommation de zoobenthos entraîne une réduction de 50 % de la biomasse des piscivores et une augmentation concomitante de 2,5 fois de l'abondance des poissons proies (c.-à-d., c'est donc dire que la consommation de zoobenthos joue un rôle clé dans la médiation du contrôle descendant pélagique). Ces résultats mettent en lumière le rôle des liens benthiques–pélagiques dans la régulation de la trophodynamique et soulignent la valeur des approches qui englobent tout l'écosystème dans l'étude des réseaux alimentaires.

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Introduction

Modern food web ecology has focused predominantly on interaction strengths (Paine 1992; Berlow et al. 2004) and the importance of top-down (predation) and bottom-up (resources) factors in determining the distribution of biomass at different trophic levels (referred to here as trophic dynamics) (Power 1992; Carpenter et al. 2001; Shurin et al. 2002). The dominance of trophic dynamics in food web ecology (e.g., Paine 1980) has diverted efforts from the elucidation of pathways of energy flow in ecosystems (food web energetics), with the result that important energy and nutrient conduits in food webs may go unrecognized. However, spatial food web subsidies, defined as the movement of organisms, energy, and materials across traditionally defined ecological or habitat boundaries, are energetically important in a wide range of ecosystems (Polis et al. 1997). Recent studies in desert (Polis and Hurd 1996), riparian (Power et al. 2004), marine (Bustamante et al. 1995; Menge 2004), and Arctic coastal (Jefferies 2000; Jefferies et al. 2004) ecosystems demonstrate that cross-habitat energy linkages strongly influence trophic dynamics in the subsidized habitats. The importance of cross-habitat linkages for trophic dynamics and stability is also supported by recent theoretical food web models (Huxel and McCann 1998; Post et al. 2000; Vadeboncoeur et al. 2005).

Lake ecosystems have been an important arena for testing trophic dynamic theory. In particular, lakes have been extensively used for experimental examination of trophic cascades in which changes in predator abundance propagate down the trophic chain to affect primary producer biomass (Carpenter et al. 1985; Pace et al. 1999; Carpenter et al. 2001). Studies of trophic dynamics in lakes are generally based on a conceptual food web model composed of either three or four functional trophic levels: phytoplankton, zooplankton, small-bodied prey fish (planktivores), and sometimes piscivores (Carpenter et al. 1985; Persson et al. 1992; Mittelbach et al. 1995). While this perception of lake food webs as reducible to a simple, linear pelagic food chain may seem overly simplistic, studies of trophic dynamics in lakes are often consistent with a chain-like trophic architecture (Persson et al. 1992; Jeppesen et al. 1997; Carpenter et al. 2001).

In contrast with the above studies of trophic dynamics, research on pathways of energy flow in lakes indicates a high degree of omnivory and reticulate food web structures (Schindler et al. 1996; Schindler and Scheuerell 2002; Vander Zanden and Vadeboncoeur 2002). Benthic habitats are often important contributors to whole-lake primary and secondary production (Wetzel 1979; Vadeboncoeur et al. 2002, 2003), and fish are mobile consumers that effectively exploit benthic and pelagic resources, thereby coupling these two habitats (Schindler and Scheuerell 2002; Vander Zanden and Vadeboncoeur 2002; Vanni 2002).

The above descriptions provide two differing views of lake food webs, depending on whether one takes a trophic dynamic or an energy flow perspective (Post 2002). While both perspectives have been informative on their own, the contrast between patterns of energy flow and dynamic control within lakes provides a rich opportunity for exploring linkages between trophic dynamics and energetic linkages (Schindler et al. 1996). Simultaneous consideration of these two perspectives allows examination of how the strength of benthic–pelagic coupling affects trophic dynamics in lakes.

The goal of this synthesis is to explore the consequences of benthic–pelagic energetic coupling for pelagic top-down control in lakes. Because there are few data or experimental studies that address this question, we review the available evidence for littoral piscivore – prey fish trophic control in North American north-temperate lakes. Second, we synthesize published dietary data to quantify energetic pathways for three bass species that are commonly implicated in top-down control in North American lakes. Finally, we explore the confluence of these two previous sections using a biomass dynamic model in which we perform the experiment of either allowing or prohibiting piscivore consumption of zoobenthos. This modeling exercise allows us to link the results of our two literature syntheses and explore how zoobenthivory is expected to affect top-down control in the pelagic food chain.

Patterns of trophic control

We searched the literature for published studies that examined impacts of littoral piscivorous fishes on prey fish abundance, species richness, and assemblage structure in North American north-temperate lakes. Piscivore species included smallmouth bass (*Micropterus dolomieu*), largemouth bass (*Micropterus salmoides*), rock bass (*Ambloplites rupestris*), and northern pike (*Esox lucius*). We included comparative, experimental, and long-term studies. Small-scale enclosure experiments were not included because the physical structure and food web linkages involving piscivorous fishes in natural ecosystem are likely to be disturbed in such studies (Lodge et al. 1998).

Dynamic top-down control is most convincingly demonstrated by the experimental manipulation of top predators. Littoral piscivores, particularly the above bass species, have been widely introduced into lakes well beyond their native range (Lee et al. 1980; Jackson 2002), and such introductions can be viewed as natural experiments. The impacts of these littoral piscivore introductions have been reasonably well studied and provide multiple independent tests of the effects of littoral predators on prey fish populations. We looked for evidence of both direct (predation) and indirect (behavioral) impacts of predators on prey fishes, recognizing that either can have important food web consequences (He and Kitchell 1990). Because we are examining whether littoral piscivore consumption of alterative prey (zoobenthos) increases predation on littoral prey fish, we assessed evidence for predator control at the littoral piscivore – prey fish link rather than full-on trophic cascades. This piscivore – prey fish interaction is a component of a trophic cascade, although even strong piscivore control of prey fish may not cascade down to phytoplankton due to compensatory mechanisms (Liebold 1989; McQueen et al. 1989; Hambright 1994).

We found that the littoral piscivores considered in our review generally have top-down impacts on prey fish abundance, diversity, and assemblage structure in North American north-temperate lakes (Table 1). All 16 of the studies reported a top-down impact of littoral piscivores on either prey fish abundance, diversity, or assemblage structure. Most

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Table 1. Summary of published studies examining piscivore impacts on species richness, abundance, and community structure of prey fishes.

Lake or region	Study type[a]	Predator species[b]	No. of lakes	Species richness	Prey abundance	Habitat use or behavior	Assemblage structure	Reference
Adirondack Park, New York, USA	c	SMB, LMB, NP	131	Yes	—	—	Yes	Findlay et al. 2000
East coast, USA	c	SMB, LMB, CP	203	Yes	—	—	Yes	Whittier and Kincaid 1999
East coast, USA	c	SMB, LMB, NP, CP, WP	195	Yes	—	—	Yes	Whittier et al. 1997
Gatineau Park, Quebec, Canada	c	YP, LMB, SMB, NP	37	Yes	—	—	—	Chapleau et al. 1997
Central Ontario, Canada	c	SMB, RB	9	Yes	Yes	—	—	Vander Zanden et al. 1999
Central Ontario, Canada	c	SMB	14	No	Yes	Yes	Yes	MacRae and Jackson 2001
Central Ontario, Canada	c	LMB, SMB, NP	249	—	—	—	Yes	Jackson et al. 1992
Alberta, Canada	c	NP	45	Yes	—	—	Yes	Robinson and Tonn 1989
Northern Wisconsin, USA	c	LMB	18	—	—	—	Yes	Tonn and Magnuson 1982
Central Ontario, Canada	c	LMB, SMB	2	Yes	Yes	—	—	Ramcharan et al. 1995
Northern Wisconsin, USA	c	LMB, SMB, RB, NP	43	Yes	—	—	Yes	Rahel 1984
UNDERC, Michigan, USA	e	NP	1	—	Yes	Yes	Yes	He and Kitchell 1990
UNDERC, Michigan, USA	l, e	LMB	3	—	Yes	—	—	Carpenter et al. 2001
ELA, Lakes 110 and 227, Ontario, Canada	e	NP	2	—	Yes	—	—	Elser et al. 1998
Lake St. George, Ontario, Canada	l, e	NP, LMB	1	—	Yes	—	—	McQueen et al. 1989
Wintergreen Lake, Michigan, USA	l, e	LMB	1	No	Yes	—	—	Mittelbach et al. 1995

Note: —, unable to assess piscivore impact on this variable from the published study; UNDERC, University of Notre Dame Environmental Research Center; ELA, Experimental Lakes Area.

[a]c, comparative study; e, experimental manipulation; l, long-term observational study.

[b]SMB, smallmouth bass (*Micropterus dolomieu*); LMB, largemouth bass (*Micropterus salmoides*); NP, northern pike (*Esox lucius*); CP, chain pickerel (*Esox niger*); WP, white perch (*Morone americana*); YP, yellow perch (*Perca flavescens*); RB, rock bass (*Ambloplites rupestris*).

studies reported information on only one or two of these response variables. Eight (50%) of the studies reported impacts of littoral predators on prey fish species richness, eight (50%) indicated impacts on overall prey fish abundance, and nine (56%) reported impacts on prey fish assemblage structure (Table 1). Where littoral pisicivores impacted prey fish assemblage structure, soft-rayed fishes such as cyprinids were typically replaced by less edible, spiny-rayed species such as percids and centrarchids. This compensatory response in the prey fish assemblage can dampen the magnitude of trophic control and has been forwarded as a mechanism to explain why the strength of top-down control is dissipated in some food chains (Hambright 1994). Overall, our synthesis indicates that littoral zone predators in north-temperate lakes have great potential to control prey fish abundance and assemblage composition across the wide range of conditions and lake types included in our literature review.

Patterns of energy flow

In this section, we examine dietary data from a large number of lakes to characterize pathways of energy flow that support production of three representative littoral piscivore species. Quantitative dietary data (expressed as a percentage of total gut content volume or weight) for 57 smallmouth bass populations, 25 rock bass populations, and 21 largemouth bass populations were taken from previous syntheses of the diet data literature (Vander Zanden et al. 1997; Vander Zanden and Vadeboncoeur 2002). The original published studies from which these diet data were extracted varied widely in the degree of taxonomic resolution of diet items.

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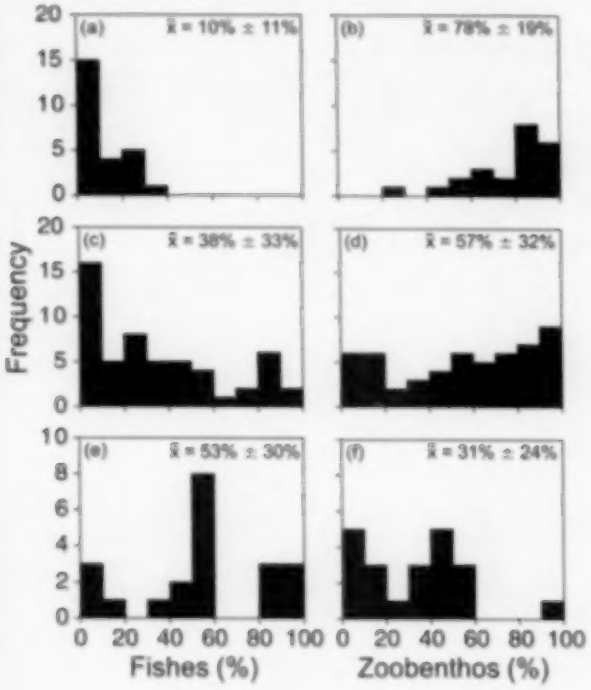
Fig. 1. Frequency distributions showing the among-population variation in consumption of fishes and zoobenthos (expressed as a percentage of total diet based on gut content studies) for (*a* and *b*) rock bass (*Ambloplites rupestris*) (n = 25 lakes), (*c* and *d*) smallmouth bass (*Micropterus dolomieu*) (n = 57 lakes), and (*e* and *f*) largemouth bass (*Micropterus salmoides*) (n = 21 lakes). Values in the top right corner of each panel are the mean (±1 SD) percent reliance on fishes or zoobenthos.



Therefore, the prey categories used in this analysis were general prey classes (zoobenthos, zooplankton, and fish) and our data set lacked detailed taxon-specific prey resolution.

A summary of diet data for the three representative littoral piscivores species (smallmouth bass, largemouth bass, and rock bass) indicates a high degree of omnivory and an important dietary role for zoobenthos. Zoobenthos were the dominant prey of rock bass (mean ± 1 SD: 78% ± 19%) and smallmouth bass (57% ± 32%). For largemouth bass, fishes and zoobenthos were both important prey items (53% ± 30% and 31% ± 24%, respectively). Frequency distributions of the percent contribution of fish and zoobenthos to bass diets also indicated that diets were highly variable among populations of a species (Fig. 1).

For each population, diet breadth was calculated as the number of prey items (from seven potential prey categories: zooplankton, mollusks, crayfish, other nonpredatory zoobenthos, other predatory zoobenthos, detritus, and other prey) that comprised more than 3% of the total gut volume (Vander Zanden et al. 1997). Diet breadth for individual populations ranged from one to six prey items (of the seven possible prey categories). Largemouth bass had the highest diet breadth (mean ± 1 SD: 3.0 ± 1.1) followed by rock bass (2.7 ± 1.1) and smallmouth bass (2.4 ± 1.0).

Synthesis and model description

Our synthesis of bass dietary data corroborates previous studies that report that littoral predators such as bass tend to have diverse and flexible diets (Schindler et al. 1997; Vander Zanden et al. 1997). The littoral predators that we examined are quite reliant on zoobenthos, while consumption of fishes tends to be energetically less important for two of the species. This important role of zoobenthos in the diets of littoral predators (energy flow perspective) contrasts with evidence for strong top-down control of prey fishes by littoral predators (trophic dynamic perspective). In this section, we use a simple model to explore the question of how the presence and magnitude of benthic prey consumption affect predator control of prey fishes. Our model considers the fate and flow of biomass within aggregated biomass pools that represent key ecological groups. In our model, these biomass pools were an idealized piscivore (hereafter referred to as piscivore), zoobenthos, and prey fish. This reliance on a simple model comprising a small number of trophic groups precludes examination of size-structured food web interactions that are common in aquatic systems (Persson and Eklov 1995). However, the model can be parameterized from available empirical data to provide easily interpretable conclusions regarding the role of alternative prey in lake food web dynamics.

The basic model structure is from the simple biomass dynamic models that form the basis of fisheries population biology (Hilborn and Walters 1992) wherein production gains from assimilated consumption are offset by losses via predation and other mortality agents. We assumed that all piscivore production is derived from consumption of fish and zoobenthos, while the production of prey fish and zoobenthos is described by a simple logistic density-dependent function. Feeding linkages between piscivores and their prey are described by a simple functional response model, and all other mortality losses are density independent. Given these structural assumptions, the model equations describing the dynamics of the state variables (P, piscivore biomass; L, prey fish biomass; B, zoobenthos biomass) are

$$(1a)\quad \frac{dP}{dt} = -ZP + AP[C_L(L,B) + C_B(L,B)]$$

$$(1b)\quad \frac{dL}{dt} = (R_{L\max} - \beta_L L)L - M_{oL}L - C_L(L,B)P$$

$$(1c)\quad \frac{dB}{dt} = (R_{B\max} - \beta_B B)B - M_{oB}B - C_B(L,B)P$$

where C_i (L,B) is the functional response of the predator to prey type i, Z is the sum of mortality and mass-specific metabolism of the predator, A is assimilation efficiency, $R_{i\max}$ is the maximum mass-specific production rate of prey type i, β_i indicates density dependence of R_i (equivalent to r/K in a logistic equation) for prey type i, and M_{oi} is mass losses due to other mortality and metabolism.

We assume that the functional response follows a Holling type II model:

$$(2a)\quad C_L(L,B) = \frac{C_{\max}a_L L}{C_{\max} + a_L L + a_B B}$$

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$$(2b) \quad C_p(L,B) = \frac{C_{max} a_B B}{C_{max} + a_L L + a_B B}$$

where a_L and a_B are the attack rates on prey fish and zoobenthos, respectively. This widely used functional response model does not consider reductions in feeding that might accompany prey refuging behavior (e.g., the foraging arena concept). This activity is known to induce predator dependence into the functional response (Abrams and Walters 1996) and to subsequently dampen top-down control (Essington and Hansson 2004). However, the aforementioned literature review indicated that piscivores do indeed exert top-down control of prey fishes, suggesting that the exchange of prey fish between vulnerable and refuge habitats is sufficiently rapid that the above approximation is reasonable. The form of the functional response on zoobenthos does not affect our analyses because our modeling perturbation compared changes in predicted steady state when there was no zoobenthos feeding (attack rate a_B equals zero). Under this condition, the functional response is always equal to zero regardless of the form of the model.

The challenge in deriving parameter estimates for this model lies in the fact that many of the parameters are not directly observable (e.g., attack rates and density-dependent parameters). Our strategy to overcome this challenge was to use available information on feeding rates, steady-state biomasses, production rates, and feeding habits and use this information to find the parameter values that are consistent with this information (Fig. 2). This approach is analogous to that used in other widely adopted model applications (e.g., EcoPath with EcoSim; Walters et al. 2000). The steady-state assumption implicit in our calculations is valid provided that the input data are not collected from lakes whose communities are radically displaced from their steady-state conditions.

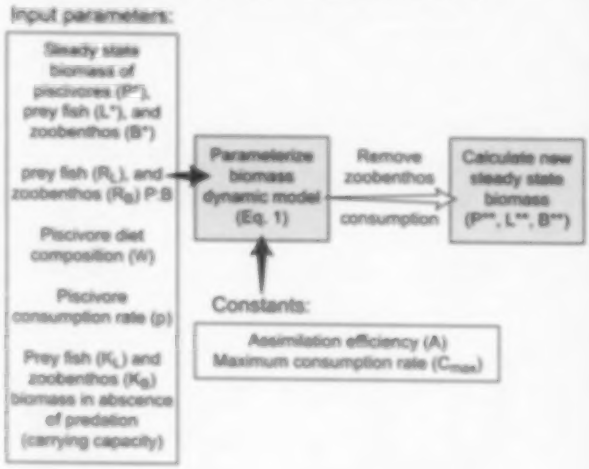
The required input data were (*i*) steady-state biomasses (P^*, L^*, and B^*), (*ii*) steady-state net production to biomass ratios of prey fish and zoobenthos (R_L^* and R_B^*), (*iii*) proportional contribution of prey fish and zoobenthos to piscivore diets (ϕ_L and ϕ_B, respectively) at steady state, (*iv*) predator consumption rate expressed as a proportion (p) of the maximum consumption rate C_{max}, and (*v*) prey biomass in the absence of predation (K_L and K_B) (Fig. 2).

These five sources of input data are sufficient to estimate all parameters in eqs. 1 and 2. At steady state, predator mortality must equal net production, so $Z = ApC_{max}$. For prey at steady state, production must equal mortality so M_{oL} equals the difference between R_L^* and predation mortality and predation mortality equals $pC_{max}P^*\phi_L/N_L^*$. When prey are at their carrying capacity (no predation), production ($R_{L\,max} - \beta_L K_L$) must equal M_{oL}. Because production minus predation also equals R^* at the specified steady-state biomass, we can therefore solve for $\beta_L = \phi_L pC_{max}P^*/[L^*(K_L - L^*)]$ and $\beta_B = \phi_B pC_{max}P^*/[B^*(K_B - B^*)]$. Given these density-dependent parameters, then $R_{max} = R_i^* + \beta_i K_i$.

To solve the functional response parameters, we recognize that at the steady-state condition, $p\phi_L = (a_L L^*)/(C_{max} + a_L L^* + a_B B^*)$ and $p\phi_B = (a_B B^*)/(C_{max} + a_L L^* + a_B B^*)$. The attack rate coefficients are therefore given by

$$(3a) \quad a_L = \frac{\phi_L pC_{max}}{L^*(1 - \phi_L p - \phi_B p)}$$

Fig. 2. Modeling approach used to compare the steady-state biomass of prey fish with and without piscivores consumption of zoobenthos. The model was run 1000 times with input parameter values randomly drawn from normal distributions with means shown in Table 2 and a coefficient of variation of 0.3.


Input parameters:
Steady state biomass of piscivores (P*), prey fish (L*), and zoobenthos (B*)
prey fish (R_L), and zoobenthos (R_B) P:B
Piscivore diet composition (W)
Piscivore consumption rate (p)
Prey fish (K_L) and zoobenthos (K_B) biomass in abscence of predation (carrying capacity)
Parameterize biomass dynamic model (Eq. 1)
Remove zoobenthos consumption
Calculate new steady state biomass (P**, L**, B**)
Constants:
Assimilation efficiency (A)
Maximum consumption rate (C_{max})

$$(3b) \quad a_B = \frac{a_L \phi_B L^*}{\phi_L B^*}$$

We used these parameter estimates to determine the steady-state biomass of piscivores, prey fish, and zoobenthos if there were no benthic energy subsidies to piscivores (Fig. 2). Steady-state biomasses under these conditions (L^{**}, P^{**}, and B^{**}) were determined by setting a_B equal to zero and solving eq. 1. Provided that all state variables are greater than zero (true when $R_{L\,max} > \beta_L L^*/\phi_L + M_{oL}$), then the new steady states are

$$(4a) \quad L^{**} = \frac{ZC_{max}}{Aa_L C_{max} - Za_L}$$

$$(4b) \quad P^{**} = \frac{(R_{L\,max} - \beta_L L^{**} - M_{oL})(C_{max} + a_L L^*)}{a_L C_{max}}$$

$$(4c) \quad B^{**} = K_B$$

When $R_{L\,max} < \beta_L L^*/\phi_L + M_{oL}$, predator biomass becomes zero and $L^{**} = K_L$.

Input data

Parameters for the above model were taken from various sources (Table 2). The steady-state biomass values for prey fish, piscivores, and zoobenthos in the presence and absence of piscivores were taken from Ramcharan et al. (1995), who compared the biomasses of these groups in two nearby lakes with contrasting food web structures. The nominal R^* for prey fish was the average value of lake-dwelling cyprinids from Randall and Minns (2000). The R^* for zoobenthos was the mean of published values from Waters (1969) and Banse and Mosher (1980). The nominal value for p (0.4) was taken from Essington et al. (2000), who estimated this parameter for over 400 individual largemouth bass in lakes in northern Wisconsin. The C_{max} was set to 10·year^{-1}, which is approxi-

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Table 2. Model input parameters, description, nominal values, and nominal value source(s) used in the model simulations.

Input parameter	Description	Nominal value	Source(s)
P^*	Steady-state piscivore biomass ($g \cdot m^{-2}$)	0.60	Ramcharan et al. 1995
L^*	Steady-state planktivore biomass in presence of piscivores ($g \cdot m^{-2}$)	0.38	Ramcharan et al. 1995
B^*	Steady-state zoobenthos biomass in presence of piscivores ($g \cdot m^{-2}$)	5.10	Ramcharan et al. 1995
R_L^*	Planktivore net production to biomass ratio at steady state ($year^{-1}$)	2.17	Randall and Minns 2000
R_B^*	Zoobenthos net production to biomass ratio at steady state ($year^{-1}$)	3.80	Banse and Mosher 1980; Waters 1969
$\bar{P}$	Proportion of predators' maximum consumption rate	0.30	Essington et al. 2000
Φ_L	Proportion of planktivores in diet	0.45	This study
Φ_B	Proportion of zoobenthos in diet	0.55	This study
K_L	Steady-state planktivore biomass in the absence of piscivores ($g \cdot m^{-2}$)	2.00	Ramcharan et al. 1995
K_B	Steady-state zoobenthos biomass in the absence of piscivores ($g \cdot m^{-2}$)	7.70	Ramcharan et al. 1995

mately one half the maximum rate for a piscivorous centrarchid at its optimal temperature (Hanson et al. 1997). The 50% reduction therefore reflects realized temperatures likely experienced by piscivores in the north-temperate lakes from which other parameters were derived. The nominal values of Φ_i of 0.45 for fish and 0.55 for zoobenthos are representative for a generalized littoral predator based on the diet data presented here. We assumed that assimilation efficiency (A) was equal to 0.65, a commonly observed value (Hanson et al. 1997).

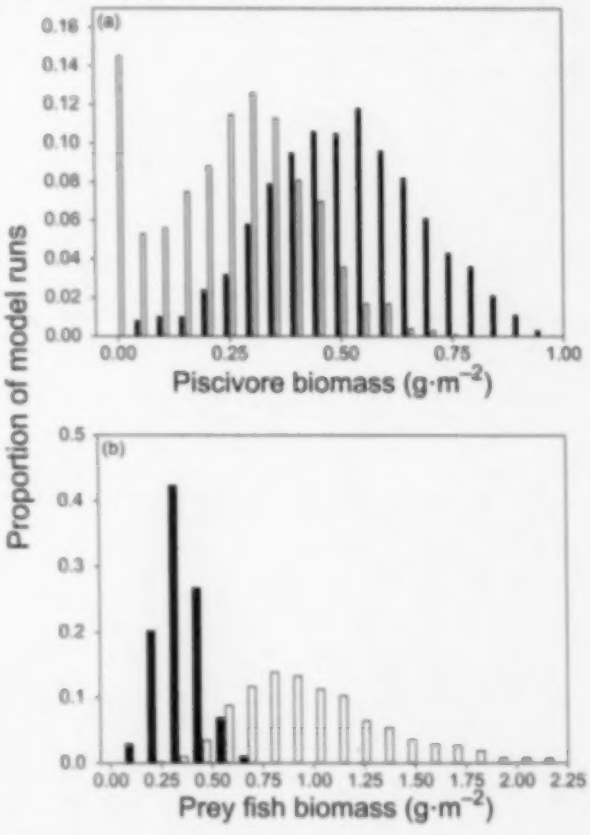
Because these are relatively imprecise parameter estimates, we assumed that each input value (Table 2) followed a normal distribution with a coefficient of variation equal to 30%. We then performed 1000 simulations in which we randomly selected parameter values from these probability distribution functions, solved for the model parameters, and then solved for the new piscivore and prey fish biomasses in the absence of zoobenthivory (P^{**} and L^{**}). Parameter sets that contained biologically implausible parameter values (e.g., negative values) were discarded.

Model results

The modeling results support the notion that zoobenthivory augments the strength of piscivore top-down control of prey fishes. There were sharp reductions in piscivore abundance in the absence of zoobenthivory. Notably, piscivore abundance was zero in the absence of zoobenthivory in 15% of all simulations (Fig. 3*a*), indicating that prey fish production was insufficient to support a piscivore population. On average, piscivore abundance was 50% less in model runs without benthic feeding (Fig. 3*a*). These reductions in piscivore populations resulted in marked increases in prey fish biomass (Fig. 3*b*). The prey fish biomass ratio (prey fish biomass without benthic energy consumption to prey fish biomass with benthic consumption) ranged from 1.06 to 10 and averaged 2.5 (i.e., on average, prey fish biomass was 2.5 times higher when piscivores were denied access to benthic prey).

The variation in model results was attributable largely to variation in the baseline contribution of zoobenthos to piscivore diets (Fig. 4). Analytically, the prey fish biomass ratio (the factor by which prey fish biomass increases in response to the loss of the benthic linkage) is equal to the inverse of the input parameter Φ_B (where Φ_B is the original

Fig. 3. Frequency distribution showing the proportion of model outcomes resulting in a given steady-state biomass of (*a*) piscivores and (*b*) prey fish. Solid bars are for model runs in which piscivores consumed zoobenthos; open bars are for model runs in which piscivores did not consume zoobenthos. Distributions were generated by randomly drawing parameter values from normal distributions with a mean value equal to the nominal values and assuming a coefficient of variation of 0.3 for each parameter.



contribution of benthos to piscivore diets), which is the accelerating upper bound of the prey fish biomass ratio (Fig. 4). However, in some cases, the new piscivore biomass

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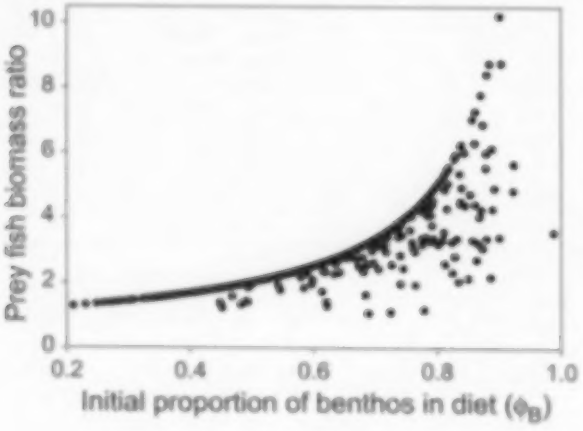
Fig. 4. Relationship between piscivore zoobenthivory (initial proportion of zoobenthos in the bass diet) and the prey fish biomass ratio (prey fish biomass without benthic energy consumption to prey fish biomass with benthic consumption) from the model output.



was zero when denied access to zoobenthic prey. When this occurred, the prey fish biomass ratio equaled K_t/L^∞, and points fell below the upper limit in Fig. 4.

Discussion

What are the dynamic consequences of a top predator deriving energy from multiple or alternative trophic pathways? One possible result is that prey consumption is spread across multiple prey, thereby reducing predation rates on any one prey item (Link 2002). An alternative view is that top-down control can become intensified by consumption of alternative prey, analogous to the idea that food web subsidies are important in driving trophic dynamics (Polis et al. 1997). Our literature syntheses indicated that littoral piscivores exert strong top-down trophic control of prey fish but that zoobenthos are of critical energetic importance to piscivores. In real ecosystems, are these two processes linked such that pelagic top-down control is strengthened in systems dominated by benthic energy flow? Because this question has not been specifically tested, we explored this question using a biomass dynamic model in which we perform the experiment of prohibiting consumption of benthic prey. Our model results indicated that given metabolic, consumption, and production rates typical for these food web components, piscivores are strongly dependent on zoobenthic prey to sustain their production. In the absence of alternative (benthic) energy sources, top-down control of prey fish biomass was substantially weakened.

Like all models, our analysis was a simplification of reality that omitted a considerable amount of biological detail. For example, our model did not consider size-structured interactions (De Roos and Persson 2002) that give rise to ontogenetic diet shifts from zooplanktivory to zoobenthivory to piscivory as individuals outgrow gape limitations (Werner and Gilliam 1984). Our model only considered the dynamics of the component of the piscivore population that regulates prey fish abundance directly. It is possible that ontogenetic diet shifts even enhance the dynamic importance of zoobenthic energy subsidies. Juvenile bass often compete with the prey fish. If zoobenthic energy pathways act to increase densities of adult bass, which in turn reduce the densities of prey fish, juvenile bass are released from competition. The result is to maintain high bass recruitment rates such that bass population size is limited by resources rather than recruitment (Walters and Kitchell 2001).

A wide range of factors will affect the outcome of piscivore – prey fish interactions. We limited our diet analysis to three common bass species. These littoral piscivores differ greatly in their foraging preferences, efficiency, and habitat use (Scott and Crossman 1973), which should translate into differences in patterns of trophic control of prey fishes. A diversity of fish species is included in our prey fish category. While these fishes are generally considered planktivores and exert top-down control of zooplankton, these fishes also consume a variety of other prey items such as zoobenthos, periphyton, and detritus (Schindler et al. 1993). Prey fish consumption of alternative resources has the opposite effect of subsidies to piscivores and would act to dampen the strength of top-down control (Stein et al. 1995). However, Ramcharan et al. (1995) reported that zoobenthic biomass was higher in a planktivore-dominated systems compared with a piscivore-dominated system, indicating piscivore, rather than prey fish, control of zoobenthos.

Littoral habitat, anthropogenic disturbances, and lake size may also influence benthic–pelagic coupling and piscivore – prey fish dynamics. Macrophytes and fallen trees (course woody habitat) create a refuge for invertebrates and prey fish, decreasing prey vulnerability and potentially reducing the magnitude of top-down control. Lake eutrophication redistributes production from benthic to pelagic habitats (Vadeboncoeur et al. 2003), while invasion of zebra mussels shifts ecosystem production from pelagic to benthic habitats (Strayer et al. 1999). The broader implications of these ecological changes are difficult to predict because the linkages between energy flow and trophic dynamics in lakes are poorly understood. Small lakes have a high perimeter to volume ratio, and we would predict closer coupling between benthic and pelagic energy pathways in a small lake (Schindler and Scheuerell 2002; Vadeboncoeur et al. 2002). Top-down control of zooplankton is higher in small lakes relative to large lakes, and piscivore biomanipulation is most likely to be successful in small lakes (Drenner and Hambright 1999, 2002; Jeppesen et al. 2003).

Bass and other littoral piscivores have been widely introduced beyond their native range, adversely impacting prey fish populations and threatening fish biodiversity (Whittier and Kincaid 1999; Jackson 2002). Perhaps the highly omnivorous diet of littoral piscivores contributes to their success and sustained impacts on prey fishes. After reducing populations of naïve prey fishes, introduced piscivores sustain high populations by feeding on alternative prey such as zoobenthos, thus preventing prey fish from recovering. A similar mechanism has been proposed in other systems. The brown tree snake (*Boiga irregularis*) devastated bird populations in Guam and was able to sustain high populations by feeding on alternative prey (amphibians and small mammals), thereby preventing bird populations from recovering (Savidge 1987). Other island studies report that exotic pred-

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ator (cats and foxes) impacts on native biota are highest where predator populations are sustained by feeding on exotic herbivores such as rabbits and mice (Smith and Quin 1996; Courchamp et al. 1999, 2000).

In an effort to develop tractable conceptual models of ecosystems, ecologists have often invoked the use of simple linear food chain models (Hairston et al. 1960; Oksanen et al. 1981; Hairston and Hairston 1993). In lakes, phytoplankton are often considered the only relevant primary producer, or at best, benthic and pelagic production processes have been treated as separate (Lodge et al. 1998; Vadeboncoeur et al. 2002). This approach neglects the potential role of benthic production and processes at the whole-ecosystem level (Wetzel 1979; Vadeboncoeur et al. 2001, 2002) and the diverse ways in which benthic, pelagic, and riparian habitats can be energetically and dynamically linked (Vanni 1996; Jeppesen et al. 1997; Schindler and Scheuerell 2002).

While we do not explicitly examine trophic cascades in this study, the piscivore – prey fish interactions that we examine are an important component of trophic cascades in lakes. Trophic cascades have most commonly been reported in the pelagic zone of lakes. This has led to the suggestion that trophic cascades are predominantly aquatic phenomena due to the simple, chain-like structure of aquatic food webs (Strong 1992). Trophic cascades may really be more common and more detectable in lakes than in terrestrial systems (Shurin et al. 2002), but aquatic food chains are not particularly simple in structure (Power 2000). In fact, we would suggest the opposite: that lake food webs are reticulate and pelagic trophic cascades in lakes may be bolstered by energetic links to benthic habitats.

Several recent reviews have examined trophic cascades and biomanipulation in lakes (McQueen 1998; Drenner and Hambright 1999, 2002). These studies specifically addressed how fish manipulations such as piscivore additions improve water quality or phytoplankton biomass (Carpenter et al. 1985, 2001). None of these recent reviews specifically examined the impacts of piscivores on prey fish abundances or assemblages, nor did they discuss the role of benthic–pelagic linkages. The general conclusion of these reviews was that fish biomanipulations cascaded down the food chain to affect phytoplankton in some cases and under certain conditions. Small lakes are more likely to exhibit trophic cascades. While it may simply be easier to effectively manipulate small ecosystems, another explanation is that the stronger benthic–pelagic linkages in small lakes intensify trophic interactions and top-down control. If benthic–pelagic linkages play a role in mediating trophic cascades, this knowledge should be useful for predicting the conditions under which lake biomanipulation is likely to be successful.

The idea that top-down control can be subsidized by allochthonous energy inputs has been of recent interest to ecologists (Polis et al. 1997, 2000; Courchamp et al. 2000). Is it appropriate to describe this interaction as a benthic "subsidy" to pelagic trophic dynamics? What is defined as a subsidy clearly depends on the scale at which the system itself is defined (Schindler et al. 1996). From the perspective of lakes as phytoplankton-based food chains, energetic linkages to the zoobenthos may be viewed as a benthic subsidy. This view perpetuates an artificial divide between pelagic and benthic habitats in lakes. We hope to promote a whole-ecosystem view of lakes in which benthic and pelagic habitats and production are inextricably linked in a reticulate food web (Schindler and Scheuerell 2002; Vadeboncoeur et al. 2002). In fact, this integrated, holistic view of lake ecosystems has strong historical roots, dating back to Lindeman's (1942) and Forbes' (1887) highly integrated depiction of lake food webs. Early fisheries biologists also recognized the energetic importance of benthic secondary production to fish production (Rawson 1930, 1952). This holistic view of lakes has been overshadowed by a predominantly pelagic research focus in the 60 years since Lindeman's (1942) seminal work, although limnologists are now reexploring benthic–pelagic coupling in lakes and its implications for lake productivity (Vanni and Layne 1997; Vanni 2002) and food web dynamics (Schindler et al. 1996; Schindler and Scheuerell 2002). While we argue for the inseparability of benthic and pelagic habitats in lakes, comparative studies combined with experimental manipulations of energy pathways will ultimately be required to elucidate the interplay between energy flow and trophic dynamics in lakes.

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PERSPECTIVE / PERSPECTIVE

Ecology of the Lake Huron fish community, 1970–1999[1]

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Abstract: We review the status of the Lake Huron fish community between 1970 and 1999 and explore the effects of key stressors. Offshore waters changed little in terms of nutrient enrichment, while phosphorus levels declined in inner Saginaw Bay. Introduced mussels (*Dreissena* spp.) proliferated and may have caused a decline in *Diporeia* spp. This introduction could have caused a decline in lake whitefish (*Coregonus clupeaformis*) growth and condition, with serious repercussions for commercial fisheries. *Bythotrephes*, an exotic predatory cladoceran, and other new exotics may be influencing the fish community. Sea lampreys (*Petromyzon marinus*) remained prevalent, but intensive control efforts on the St. Mary's River may reduce their predation on salmonines. Overfishing was less of a problem than in the past, although fishing continued to reduce the amount of lake trout (*Salvelinus namaycush*) spawning biomass resulting from hatchery-reared fish planted to rehabilitate this species. Massive stocking programs have increased the abundance of top predators, but lake trout were rehabilitated in only one area. Successful lake trout rehabilitation may require lower densities of introduced pelagic prey fish than were seen in the 1990s, along with continued stocking of hatchery-reared lake trout and control of sea lamprey. Such reductions in prey fish could limit Pacific salmon (*Oncorhynchus* spp.) fisheries.

Résumé : Nous faisons le point sur l'état de la communauté de poissons du lac Huron de 1970 à 1999 et nous étudions les effets des principaux facteurs de stress. Les eaux du large ont connu peu de changement en ce qui a trait à l'enrichissement en nutriments, alors que les concentrations de phosphore ont diminué dans la baie de Saginaw intérieure. Les moules introduites (*Dreissena* spp.) ont proliféré et ont peut-être causé un déclin de *Diporeia* spp. Cette introduction peut avoir causé une diminution de la croissance et de la condition du corégone de lac (*Coregonus clupeaformis*), ce qui a eu des répercutions graves sur les pêches commerciales. *Bythotrephes*, un cladocère prédateur exotique, et d'autres espèces exotiques nouvelles peuvent peut-être influencer la communauté de poissons. Les grandes lamproies marines (*Petromyzon marinus*) restent présentes, mais des efforts considérables de contrôle dans la rivière

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St. Mary's peuvent avoir réduit leur prédation sur les salmoninés. La surpêche est un problème moins important que par le passé, bien que la pêche ait continué de réduire la biomasse des reproducteurs chez le touladi (*Salvelinus namaycush*) provenant des élevages en pisciculture et ensemencés pour la réhabilitation de l'espèce. Des programmes d'empoissonnements massifs ont accru l'abondance des prédateurs supérieurs, mais le touladi n'a été réhabilité que dans une région. Le succès de la réhabilitation du touladi exigera peut-être des densités d'introduction de poissons pélagiques plus faibles que dans les années 1990, tout en maintenant l'empoissonnement de touladis élevés en pisciculture et le contrôle des grandes lamproies marines. De telles réductions des poissons proies pourraient limiter les pêches des saumons du Pacifique (*Oncorhynchus* spp.).

[Traduit par la Rédaction]

Introduction

The watershed of the Laurentian Great Lakes encompasses over 750 000 km^2, each of the five Great Lakes ranks among the largest 17 in the world, and Lake Huron has the world's fourth largest surface area. The water bodies that comprise Lake Huron (the main basin, the North Channel, and Georgian Bay) are partially separated by Manitoulin Island and the Bruce Peninsula (Fig. 1). Saginaw Bay is a large, shallow enbayment of the main basin. Lake Huron is connected to Lake Michigan by the Straits of Mackinac and also receives outflow from Lake Superior through the St. Mary's River. The lake is generally characterized as oligotrophic.

The Great Lakes experienced substantial anthropogenic ecological change, including changes to nutrient concentrations, habitat, and species diversity. By the 1960s, these changes had substantially degraded the Great Lakes for human use, including reductions in the abundance of fishable populations. The 1971 Salmonid Communities of Oligotrophic Lakes (SCOL-1) symposium was aimed at describing changes in the lakes: identifying the effects of cultural eutrophication, fishery exploitation, and fish introductions and predicting future responses (Loftus and Regier 1972). The 1972 and 1978 Great Lakes Water Quality Agreements (GLWQA) between Canada and the United States were directed specifically at reducing nutrient and contaminant loads.

By the start of the 1970s, the Lake Huron fish community was highly disturbed (Berst and Spangler 1972). Lake trout (*Salvelinus namaycush*), once the dominant predator, was nearly extirpated with only two extant, localized populations remaining, both in Georgian Bay. Burbot (*Lota lota*), another important native predator, had declined in abundance. Populations of lake herring (*Coregonus artedi*), lake whitefish (*Coregonus clupeaformis*), and bloater (*Coregonus hoyi*) were greatly reduced in abundance and in their contributions to the fisheries. Other deepwater ciscoes (*Coregonus* spp.) were greatly reduced in abundance or extirpated (Eshenroder and Burnham-Curtis 1999). Major stressors identified as the root causes of these changes were commercial fishing and the invasion of the sea lamprey (*Petromyzon marinus*).

Although fishery declines were well underway by the time sea lamprey abundance reached high levels, their large numbers were viewed as a major impediment to recovery. This marine species selectively attacks and attaches to larger-bodied fishes, and its removal of bodily fluids frequently degrades blood quality so much that attacked fish die. The persistence of other larger-bodied fishes, such as burbot, suckers (Catostomidae), lake whitefish, and exotic rainbow trout (*Oncorhynchus mykiss*), was viewed as resulting from their life history strategy of reproducing at smaller sizes, before sea lamprey induced mortality became too severe (Berst and Spangler 1972). The selective removal of large-bodied fishes favored small-bodied exotic planktivores, alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*), which became extremely abundant (Berst and Spangler 1973). Berst and Spangler (1973) saw a recovery of the Lake Huron fish community as hinging on the successful control of sea lampreys and the reestablishment of climax predators. At the time of the SCOL-1 symposium, mass stocking of Pacific salmon and lake trout had just begun, and peak stocking levels (and recreational fishery harvests) were in the future. Although effective chemical methods for killing larval sea lampreys were available earlier, lake-wide treatment had only recently occurred and a response to the treatment had not been evaluated. Berst and Spangler (1972) viewed the effects of elevated nutrients and contaminants as relatively minor, although they expressed concerns that these effects could be understated owing to substantial time lags associated with the relationship between open-water concentrations and elevated loadings. They were hopeful that the forthcoming GLWQA would prevent further deterioration of the aquatic environment.

Much has changed in the Lake Huron ecosystem during the more than 30 years since the SCOL-1 symposium. The desired lake-wide recovery of self-sustaining lake trout populations has not occurred (Eshenroder et al. 1995), although massive stocking of Pacific salmon and lake trout led to a substantial increase in the abundance of top predators. In turn, populations of predator fish supported valuable recreational fisheries (Bence and Smith 1999). Recovery of lake whitefish populations led to increased commercial fishing effort and associated mortality of lake trout, which are often caught as bycatch in that fishery (Brown et al. 1999). Lake-wide chemical treatment of tributary streams initially led to a substantial decrease in the abundance of sea lampreys, but increased survival of juvenile sea lampreys originating from the untreated St. Mary's River followed this decline. As a consequence of the GLWQA, both nutrient and contaminant loadings to Lake Huron decreased. A number of additional exotic species invaded since 1971, but the full effects of these new species are still uncertain. We review these changes, focusing on the major species, and make a prognosis for the future.

Nutrient loading

Based on studies of total dissolved solids, transparency, and dissolved oxygen, the open waters of Lake Huron are

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Fig. 1. Major basins and landmarks of Lake Huron. The boundary between US and Canadian waters (dotted line) and inner and outer Saginaw Bay (broken lines) are shown.

oligotrophic despite concerns in the early 1970s that the lake's water quality was deteriorating (Dobson et al. 1974). Declines in important recreational and commercial fishes in Saginaw Bay during the 1950s and 1960s led to concerns that human activities were altering productivity in nearshore mesotrophic areas (Beeton 1969). Cultural eutrophication and pollution were most severe in dense industrial and agricultural areas, and phosphorus loading was recognized as the major factor. First signed in 1972, the GLWQA brought commitments from the United States and Canada to restore and maintain the chemical, physical, and biological integrity of the Great Lakes ecosystem (International Joint Commission 1972) and, when revised in 1978, established the current Lake Huron phosphorus concentration and loading targets. Through programs that controlled nutrient inputs, phosphorus loading fell from 5.1 million kg·year^{-1} in 1978 to below the GLWQA target, 4.3 million kg·year^{-1}, by 1981 and has remained below the target in all but a few years (Beeton et al. 1999).

The feared increase in open-lake phosphorus concentrations did not materialize despite the higher loadings of the 1960s and 1970s, nor was a decrease in concentrations evident subsequent to decreases in loadings (Stevens et al. 1985). From 1978 to 1995, open-lake spring total phosphorus concentrations were stable and, with one minor exception, remained below the target level of 5.0 mg·m^{-3} (Fahnenstiel et al. 1998). During the period prior to and subsequent to the reduction in phosphorus loadings, a number of studies classified all three basins of Lake Huron as oligotrophic (Beeton and Saylor 1995).

Several nearshore areas, including Saginaw Bay and Georgian Bay, are characterized by higher phosphorus concentrations than are present in the main basin of Lake Huron (Nicholls et al. 2001). The largest is Saginaw Bay, where spring total phosphorus concentrations reached as high as 60.0 mg·m^{-3} by the early to mid-1970s (Smith et al. 1977). Phosphorus concentrations in the bay declined but remain substantially higher than in open waters of the lake. From 1991 through 1993, total phosphorus in the bay, averaged over April–October, decreased from 24.6 to 16.2 mg·m^{-3}, a change attributed to increased numbers of zebra mussels (*Dreissena polymorpha*) acting as a nutrient sink (Johengen et al. 1995). Clearly, the GLWQA target of 15 mg·m^{-3} remains a challenge in Saginaw Bay. Similarly, despite loading

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reductions in Georgian Bay, total phosphorus will have to be monitored because a 1 $mg \cdot m^{-3}$ increase could result in nuisance phytoplankton growths.

Nitrate is unlikely to be limiting in Lake Huron and the nutrient environment of the lake is favorable for diatoms and green algae. Increasing levels of nitrate plus nitrite have been reported across the Great Lakes for the past two decades. A significant increase in nitrate plus nitrite was observed in Lake Huron (Stevens et al. 1985), and the nitrogen to phosphorus ratio increased from an already high value of 53 in 1971 to 72 in 1991.

Phytoplankton

Phytoplankton community structure in Lake Huron changed very little from the late 1980s through the mid-1990s; all major groups were similarly abundant over the two periods (Makarewicz and Bertram 1991). Forty common species and varieties account for most of the abundance and biomass of phytoplankton in the lake (Makarewicz and Bertram 1991). Because of low phosphorus concentrations and high nitrogen to phosphorus ratios, Diatomeae predominate except in Saginaw Bay (Stevenson 1985; Makarewicz and Bertram 1991; Munawar et al. 1995). Species composition varies seasonally and between basins (Stevenson 1985).

Low and untrending phytoplankton biomasses are expected in offshore waters of the Great Lakes, and the limited time series data for the main basin of Lake Huron support this expectation. In 1971, phytoplankton biomass in the main basin was low, averaging 0.4–0.79 $g \cdot m^{-3}$ at most stations, but was moderately high at some inshore stations. Biomass varied seasonally with the highest values during spring diatom blooms (Munawar and Munawar 1982). From 1983 to 1985, biomass at offshore stations (measured by composite samples taken at 1, 5, 10, and 20 m) in the main basin remained low and ranged from 0.34 to 0.41 $g \cdot m^{-3}$, with spring or early summer peaks. Phytoplankton biomass remained low, averaging less than 0.4 $g \cdot m^{-3}$ during 1998–1999.

Primary production has not increased appreciably from the time of the SCOL-1 symposium. Lake Huron ranks as the second lowest of the Great Lakes in terms of chlorophyll *a* and primary productivity (Beeton et al. 1999). With the exception of Saginaw Bay, chlorophyll *a* values in the main basin in the early 1970s rarely exceeded 3 $mg \cdot m^{-3}$ (Munawar and Munawar 1982). In 1974, chlorophyll concentrations ranged from 2.1 (main basin) to 0.91 (Georgian Bay) (International Joint Commission 1977) and were lower than or as low as in 1980 (Moll et al. 1985) and 1985 (Makarewicz et al. 1989).

Benthic invertebrates

Any change in total abundance of benthic invertebrates between the early 1970s and 1997–1998 is obscured by large variations among sampling locations and among years (Table 1). The composition of the benthic community, however, clearly did change during this period. The benthos of the main basin is typical of that found in offshore waters of the other upper lakes. At depths below the thermocline (>30 m), amphipods (*Diporeia* spp.) are the predominant form followed by oligochaetes, sphaeriids, and chironomids. *Diporeia* increased from 43%–72% in 1970–1972 to 77%–83% in 1997–1998, while oligochaetes declined from 18%–42% to only 12%–18% over the same years.

Peterson-grab surveys in the 1950s and in 1965 indicate that the recent community shift to *Diporeia* is a return to an earlier state (Teter 1960; Schuytema and Powers 1966). Although these early data cannot be quantitatively compared with the more recent Ponar-based estimates (the Peterson-grab is less efficient than the Ponar), they can be used to compare community composition across years. In the 1950s, *Diporeia* and oligochaetes accounted for 81% and 9%, respectively, of total numbers as compared with 48%–76% *Diporeia* (depending on sampling location) and 22%–30% oligochaetes in 1965. Abundance and community composition of the offshore benthos in Georgian Bay and the North Channel, surveyed extensively only in 1973 (Cook and Johnson 1976), indicate similar conditions as reported for the main basin during the same period.

The biggest change in the macroinvertebrate community of inner Saginaw Bay (Fig. 1) prior to the early 1970s was the decline in populations of the mayfly *Hexagenia*. In the mid-1950s, abundance of *Hexagenia* in soft sediments was 63 m^{-2}, but by the mid-1960s, the population fell to near zero (Schneider et al. 1969). The decline was attributed to increased eutrophication and oxygen depletion in the near-bottom waters. This organism is still rare in Saginaw Bay (Nalepa et al. 2003).

Abundances of the three major macroinvertebrate groups changed markedly in inner Saginaw Bay (Fig. 1) between the early 1970s and the 1990s (Table 2). Over this period, oligochaetes and chironomids declined in both hard and soft substrates, while amphipods (*Gammarus* spp.) increased. These changes most likely reflect phosphorus control and the introduction and rapid expansion of zebra mussels. First found in the bay in 1990, zebra mussels had densities of 2000 – 34 000 m^{-2} at inner bay sites with hard substrates during 1991–1996 (Nalepa et al. 1999). The increased density of *Gammarus* spp. at hard-substrate sites in the inner bay is similar to increases found in the other Great Lakes after mussels became established (Ricciardi et al. 1997). The decline in oligochaetes and chironomids in Saginaw Bay, however, contrasts with increases in the density of these taxa reported in the same studies for the other Great Lakes. The reason for the decline of these two groups at hard-substrate sites in Saginaw Bay is not clear.

Abundances of most major benthic taxa also declined in outer Saginaw Bay (Fig. 1) between the early 1970s and the 1990s (Table 2). The decline of *Diporeia* has the greatest implication for the bay's food web. Following the establishment of zebra mussels in Lake Michigan (Nalepa et al. 1998), *Diporeia* populations declined, and the condition of fish that fed on *Diporeia* declined subsequently (Pothoven et al. 2001; Madenjian et al. 2003). *Diporeia* relies on freshly settled material (e.g., diatoms) as a food source, and zebra mussels filter and remove this material. Although food limitation has been a suspected mechanism, a clear link between the *Diporeia* population declines and reduced detrital settling rates has not been established. *Diporeia* populations declined in abundance in outer Saginaw Bay but are still abundant in the main basin (Table 1).

Mysis is important in the food webs of the Great Lakes, but its dynamics and role in Lake Huron are poorly studied.

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Table 1. Mean ± SE densities (m^{-2}) of major benthic macroinvertebrates and number of Ponar grabs (n) for the open waters of Lake Huron by depth.

	1970[a]	1971[b]	1972[c]	1997[d]	1998[d]
<30 m	$n = 8$	$n = 20$	$n = 26$		
Diporeia spp.	867±547	111±59	866±23	—	—
Oligochaeta	1495±1204	274±106	2679±590	—	—
Sphaeriidae	40±30	250±129	299±798	—	—
Chironomidae	124±79	60±15	407±81	—	—
Total	2564±1858	806±276	4427±828	—	—
30–50 m	$n = 3$	$n = 10$	$n = 14$	$n = 2$	$n = 2$
Diporeia spp.	2612±955	471±187	5418±714	2610±469	3429±414
Oligochaeta	674±307	502±149	2870±414	617±109	493±182
Sphaeriidae	394±151	194±56	1324±211	89±46	61±4
Chironomidae	26±23	31±10	334±116	73±16	124±3
Total	3764±1160	1209±360	9956±1244	3388±607	4107±239
50–90 m	$n = 7$	$n = 18$	$n = 12$	$n = 5$	$n = 5$
Diporeia spp.	2145±390	500±82	5393±648	3353±464	2274±696
Oligochaeta	683±200	289±51	1484±364	516±115	368±107
Sphaeriidae	112±40	346±224	538±84	231±85	185±63
Chironomidae	39±15	104±41	73±14	31±8	33±14
Total	3007±459	1167±256	7489±1023	4130±559	2860±853
>90 m		$n = 16$		$n = 3$	$n = 3$
Diporeia spp.	—	490±82	—	4266±738	2949±570
Oligochaeta	—	212±64	—	520±254	340±154
Sphaeriidae	—	33±16	—	33±8	25±4
Chironomidae	—	11±3	—	98±33	59±26
Total	—	745±109	—	4917±993	3373±584

[a]Schelske and Roth (1973).
[b]Shrivastava (1974).
[c]S. Morley, Department of Zoology, North Carolina State University, 4105 North Gardner Hall, Raleigh, NC 27695, USA, unpublished data.
[d]Marc Tuchman, Great Lakes National Program Office, Environmental Protection Agency, 77 West Jackson Boulevard, Chicago, IL 60604, USA, unpublished data.

Carpenter et al. (1974) noted that abundance in 1971 increased with depth, that *Mysis* was scarce during summer except in the deeper waters of the northern main basin, and that their distribution was more uniform at other seasons. Sell (1982) analyzed these same data and reported an average biomass of 0.53 g dry mass·m^{-2} and production (dry) of 1.5 g·m^{-2}·$year^{-1}$. These numbers are lower than some (but not all) values that he calculated for Lake Michigan, but the deeper sampling depths in Lake Huron would result in a positive bias as compared with Lake Michigan. The production to biomass ratio of *Mysis* was similar (2.8) in both lakes.

Zooplankton

Zooplankton community composition in Lake Huron is different among the main basin, Georgian Bay, and the North Channel but similar to that in the other upper Great Lakes, particularly Lake Michigan (Barbiero et al. 2001). Lake Huron's zooplankton community has been dominated by calanoid and diaptomid copepods (Watson and Carpenter 1974; Sprules and Jin 1990; Barbiero and Tuchman 2000). Dominance varies by season, with naupli and rotifers dominating in April and diaptomids and cladocerans dominating in June and July (Evans 1986). The most abundant copepod throughout the lake is *Cyclops bicuspidatus thomasi* (Watson and Carpenter 1974).

Bythotrephes, an exotic predaceous zooplankter, which became established in Lake Huron in 1984, may be responsible for a shift to larger-bodied cladocerans during 1970–1999 (Lehman 1991; Laxson et al. 2003). The contribution of various groups of copepods differs between spring and summer, but their annual contribution to the planktonic–crustacean community composition was stable between 1970 and 2000 (Barbiero et al. 2001). In contrast, the cladoceran community during this period shifted from a predominance of bosminids to a predominance of daphnids. Daphnids accounted for less than 10% of the planktonic crustacean numbers during the 1970s and 1980s (Watson and Carpenter 1974; Evans 1986) but increased to 22% in 1988 (Sprules and Jin 1990) and to 25% in 1998 (Barbiero et al. 2001). Contributions by bosminids declined from 14% by numbers in 1988 (Sprules and Jin 1990) to 8% in 1998 (Barbiero et al. 2001).

Prey fish

In their review of Lake Huron, Berst and Spangler (1972) identified introduced rainbow smelt and alewives and native deepwater ciscoes as the dominant forage fishes. During

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Table 2. Mean ± SE abundance (m^{-2}) of major benthic macroinvertebrate groups in the inner (sites with hard and soft substrate) and outer portions of Saginaw Bay.

	1971	1987–1990	1993–1996
Inner Saginaw Bay			
Substrate: sand	$n = 3$[a]	$n = 3$[b]	$n = 3$
Oligochaeta	1436±204	1197±498	668±101
Chironomidae	764±493	267±129	186±74
Gammarus sp.	143±72	49±29	346±60
Substrate: silt	$n = 4$	$n = 4$	$n = 3$
Oligochaeta	13 662±1123	17 394±1986	1976±924
Chironomidae	2499±602	1296±213	1130±601
Gammarus sp.	6±5	1±1	11±3
Outer Saginaw Bay	$n = 9$[c]	$n = 1$[b]	–1
Diporeia spp.	1158±536	819±189	254±98
Oligochaeta	4553±1299	388±88	607±162
Sphaeriidae	549±172	288±68	168±60
Chironomidae	1688±176	218±49	420±140

Note: n is the the number of sites; 1971, prephosphorus control; 1987–1990, postphosphorus control and pre-*Dreissena*; 1993–1996, postphosphorus control and post-*Dreissena*. For outer Saginaw Bay, variability in 1971 is between sites, while variability in 1987–1996 is between years.

[a]Batchelder (1973).

[b]Nalepa et al. (2003).

[c]S. Morley, Department of Zoology, North Carolina State University, 4105 North Gardner Hall, Raleigh, NC 27695, USA, unpublished data.

1970–1999, the abundance of deepwater ciscoes diminished, while exotic prey fishes became ubiquitous. Since annual bottom-trawl prey assessments began in Lake Huron in the early 1970s, rainbow smelt and alewives have accounted for at least 60% of the catch by weight (Argyle 1982) and have become the major component in the diets of lake trout and other salmonines (Dobiesz 2003).

Following the buildup of top-predator populations in the main basin in the late 1970s to early 1980s, smaller, younger fish dominated the populations of rainbow smelt and alewives. Mean age of alewives age 1+ was 2.9 years from 1973 through 1981 but declined to 1.8 years in the mid- to late 1980s. Mean age continued declining after the late 1980s except in 1993–1995, when recruitment of several strong year-classes briefly shifted age and size structure back to older, larger fish (R.L. Argyle, unpublished data). Similarly, more than 80% of the adult rainbow smelt population is age 2 or younger, and in most years, less than 10% of the adults are older than age 3 (R.L. Argyle, unpublished data). The shift to smaller, younger alewives and rainbow smelt after the mid-1980s was accompanied by declines in adult biomass despite appearances of strong age-0 cohorts (Fig. 2). For example, age-0 alewives were abundant in 1995, but for some reason, age-3 alewives were scarce 3 years later when they should have boosted adult biomass. Age-0 cohorts of rainbow smelt were also abundant in the 1990s, but biomass of adults declined as the mean weight of adult rainbow smelt dwindled from 16 to 10 g during 1975–1999 (R.L. Argyle, unpublished data). Whether the level of predation on young alewives was sufficient to suppress recruitment is unclear. Alewives are also susceptible to overwinter mortality, particularly during harsh winters. Other climatic conditions such as fall cooling and spring warming rates can have a large impact on the success of individual year-classes (O'Gorman and Stewart 1999).

The remaining 40% of the bottom-trawl catches in the main basin comprised, in order of decreasing importance, deepwater sculpins (*Myoxocephalus thompsoni*), slimy sculpins (*Cottus cognatus*), ninespine sticklebacks (*Pungitius pungitius*), and trout-perch (*Percopsis omiscomaycus*). Of these species, only ninespine sticklebacks have been prominent in top-predator stomachs and then only in chinook salmon (*Oncorhynchus tshawytscha*) (Diana 1990). The ninespine stickleback is the only one of these four species that declined in abundance after the introduction of salmonines, whereas trout-perch abundance increased from 1973 through 1999.

Ciscoes

Lake herring

Lake herring, also known as shallow-water cisco, remained at a relatively low abundance in Lake Huron during 1970–1999, having changed little since Berst and Spangler (1973) implied that it was a victim of competition with introduced rainbow smelt. The lake herring fishery had been intensive historically only in Michigan's waters and there mostly in Saginaw Bay where the fishery intercepted a massive spawning run (Van Oosten 1929). Dramatic changes in lake herring abundance did not occur when rainbow smelt first proliferated, although Berst and Spangler (1973) noted that lake herring populations declined as rainbow smelt numbers increased. Rainbow smelt may have contributed to declines in lake herring numbers — lake herring were most persistent where rainbow smelt densities were lowest: in the North Channel (Spangler and Collins 1992) — but whether major

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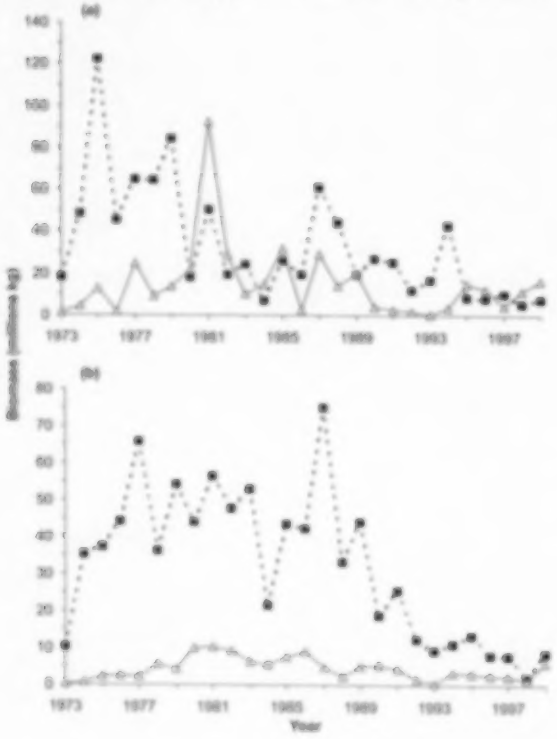
Fig. 3. Estimated biomass of adult (squares) and young-of-the-year (triangles) (*a*) alewife (*Alosa pseudoharengus*) and (*b*) rainbow smelt (*Osmerus mordax*) from 1973 to 1999 in US waters of Lake Huron. Annual systematic surveys of prey fish populations were conducted using a 12-m bottom trawl from 1973 to 1991 and a 21-m bottom trawl from 1992 to 1999. Locations, depths fished, and trawling gear are described in Argyle (1982).



interactions occurred remains obscure. Lake herring populations could no longer support major fisheries after the mid-1960s and persist now only in the northern waters of the main basin, the lower St. Mary's River, and the North Channel. These northern populations are of particular interest because they are the nearest source of colonists for depopulated areas farther south in Lake Huron. Assessment gillnetting along the south shore of Drummond Island suggests that year-class strength improved markedly in the mid-1990s. The 1993–1995 year-classes at ages 3–5 were 20 times larger than the 1988–1992 year-classes (M.P. Ebener, unpublished data). This improvement is encouraging assuming that range expansion would begin with increases in abundance of the source population.

Deepwater ciscoes

Deepwater ciscoes (commercially known as chubs) appear to have been very sensitive to pulses in fishing pressure for two reasons: (*i*) cyclic recruitment associated with female predominance made populations particularly vulnerable to collapse and (*ii*) depletion of one species did not result in a relaxation of fishing pressure as long as other deepwater ciscoe species were present to support the fishery (Smith 1968). Originally, there were six deepwater ciscoe species, but by the late 1990s, only the smallest of these species (bloater) persisted in Lake Huron. Berst and Spangler (1973) did not list deepwater ciscoes among the species whose demise they attributed solely to overfishing. At the time of their paper, a bout of intensified fishing that produced record but apparently unsustainable catches was coming to an end (Fig. 3*a*). They suggested that the record chub catches of the late 1950s and 1960s were supported by the smaller-bodied species of deepwater ciscoes, which prospered after being released from competition. Their competitors, larger-bodied fish such as lake whitefish, lake herring, and the larger-bodied species of deepwater ciscoes, had been greatly reduced in abundance by sea lamprey parasitism and fishing.

Cycles in the sex ratio and weak recruitment are well documented for Lake Michigan bloaters (TeWinkel et al. 2002). In the early part of a cycle, adult abundance is low, females predominate markedly, and recruitment is weak. In the middle of a cycle, recruitment is reestablished and the sex ratio becomes less biased as males are well represented among recruits. In the last part of a cycle, adult abundance declines, females predominate as males are winnowed by higher mortality, and recruitment nearly ceases. The bloater population in Lake Huron's main basin also appears to follow this type of cyclic behavior (Fig. 3*b*) with adult biomass increasing from low levels in the mid-1970s (Brown et al. 1987) and returning to low levels by 1998–1999.

We believe that two bouts of intensified chub fishing in Lake Huron, one that began in the late 1950s in the main basin and another that began in the 1970s in Georgian Bay, caused severe declines in population abundance, including extirpation, because both episodes coincided with the late part of a population cycle when recruitment was weak. We assume, based on Lake Michigan, that weak recruitment by itself or exaggerated female predominance can be used to mark where a population is in a cycle. In the main basin example, length frequencies of bloaters were significantly shifted towards larger fish in 1956 when intensified fishing started as compared with 1938 (before intensified fishing began) and with 1977 (when population recovery was well underway) (Fig. 3*c*). These admittedly sparse data from outer Saginaw Bay suggest that when the fishery was gearing up in the late 1950s, the chub population was in the latter half of a population cycle typified by high adult biomass and weak recruitment. This hypothesis explains how catches could decline so rapidly from record-high levels (Fig. 3*a*) — there was little replacement for the adult fish being removed by the fishery.

In the second example, which involves a period of intensified fishing on Georgian Bay chubs during the 1970s and early 1980s, growth of bloaters was faster and female predominance was high just before fishing started (Brown et al. 1987), suggesting that the population was in the early part of a cycle. Mean age of bloaters, which is positively related to female predominance (TeWinkel et al. 2002), was also high when fishing started but fell rapidly as catch per unit effort plunged in response to the fishing-up of adult chubs in the late 1970s (Fig. 3*d*). Younger fish supported the fishery into the early 1980s, indicating that by the mid-1980s, the population was still in the first half of a cycle, but apparently, recruits were too few and (or) small to stave off the plunge in catch per unit effort, which reached its nadir in the early

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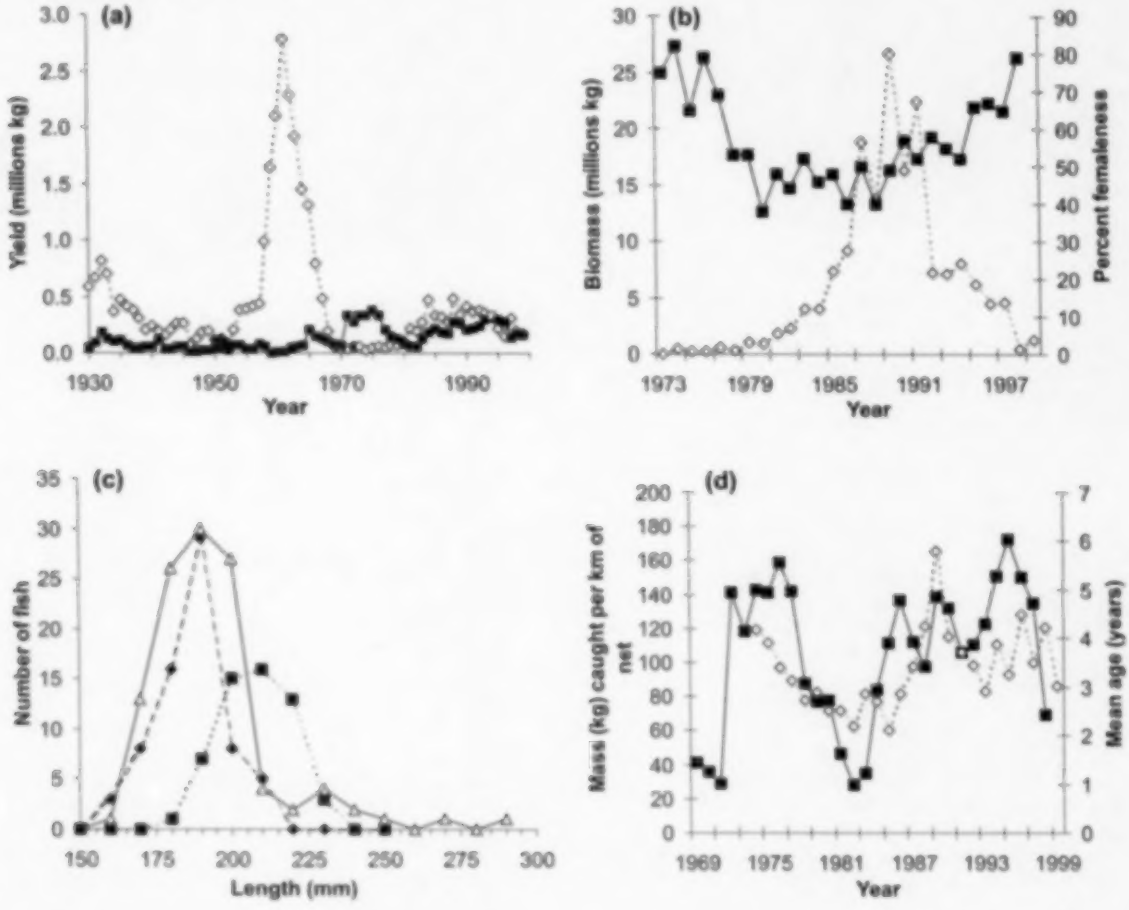
Fig. 3. Population and catch statistics for deepwater ciscoes (chubs; *Coregonus* spp.) in Lake Huron. (*a*) Commercial yield of chubs from the main basin (diamonds) of Lake Huron and Georgian Bay (squares), 1930–1999. (*b*) Estimated biomass (diamonds) and percent females (squares) for adult bloaters (*Coregonus hoyi*) (age 1+) taken in assessment bottom trawls in Lake Huron's main basin, 1973–1999 (R.L. Argyle, unpublished data). (*c*) Length–frequency distributions of bloater taken in 38-mm gill nets from outer Saginaw Bay in 1938 (diamonds), 1956 (squares), and 1979 (triangles) (R.L. Eshenroder, unpublished data). (*d*) Catch per unit effort (squares) for the commercial chub fishery and mean age of chubs (diamonds) taken in graded-mesh gill nets in Georgian Bay, 1969–1999 (L.C. Mohr, unpublished data).



1980s. These recruits, however, enabled a second bout of intensified fishing during the late 1980s and 1990s. Their presence also explains why the second bout of intensified fishing was more sustainable than the first (Fig. 3*d*) — fishery expansion coincided with the middle part of a population cycle when recruitment is stronger.

The role of rainbow smelt and alewives in the ciscoe population collapse in the Great Lakes is still debated. Berst and Spangler (1973) dismissed the alewife as an impediment to recruitment of deepwater ciscoes in the main basin of Lake Huron because they believed that alewives did not become abundant until the early 1960s, when deepwater cisco recruitment was already reduced. Carr (1962), however, reported that age-0 alewives were the predominant fish in Saginaw Bay in 1956, when intensified chub fishing in the main basin was just starting. If adult alewives were sufficiently abundant to produce a dominant year-class in 1956, we believe that they were abundant enough to interfere with a recovery of deepwater ciscoes following the bout of intensified chub fishing of the late 1950s and early 1960s. Insomuch as peak catches of chubs occurred in 1961, well after rainbow smelt became prominent, it is unlikely that rainbow smelt triggered recent (after 1956) extirpations of deepwater ciscoes in Lake Huron.

Lake whitefish

During the last two decades, lake whitefish populations were more abundant than during the Berst and Spangler (1972) review. Consistently strong reproduction occurred throughout most areas of Lake Huron beginning with the 1977 year-class and progressing through about the 1994 year-class (M.P. Ebener, unpublished data). In the Canadian waters of the main basin, the successful year-classes ended in

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1991, and by 1994, three weak year-classes led to reductions in quotas in these waters (L.C. Mohr, unpublished data).

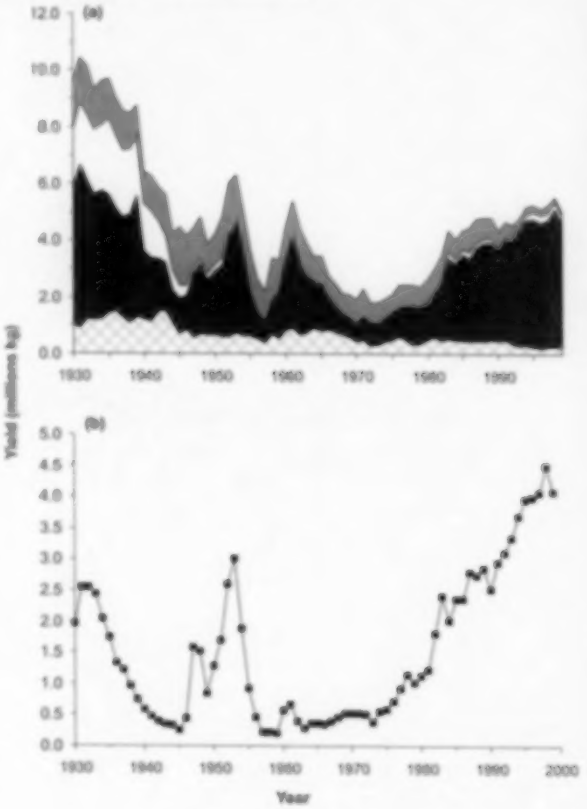
Survival of adult lake whitefish increased substantially, especially in the main basin and North Channel, after the first full round of chemical treatments of sea lamprey inhabited streams (Spangler and Collins 1980). At the same time, abundance of lake trout and chinook salmon in Lake Huron was increasing as was their predatory effects on rainbow smelt and alewives. This predation pressure likely increased the survival of lake whitefish juveniles by reducing predation, and potentially competition, between them and alewives and rainbow smelt (Ebener 1997). Favorable environmental conditions also promoted high lake whitefish egg and fry survival resulting in consistently strong year-classes that were spatially segregated and subjected to different levels of fishing and sea lamprey predation (Brown et al. 1993).

The prolonged surge in lake whitefish abundance appears to be ending. Commercial catches have peaked in the main basin (Fig. 4*a*) and lake whitefish growth is declining. In the southern main basin, where the decline in growth was most pronounced, mean weight of age-3 lake whitefish decreased from 1.10 kg in 1979 to 0.25 kg in 1998. The decline in growth was less pronounced outside the main basin. During 1976–1998, the average decrease in weight-at-age was approximately 20% in Georgian Bay and 23% in the North Channel (L.C. Mohr, unpublished data). Declines in growth were accompanied by delayed maturation. In northern US waters during 1976–1982, 50% of female lake whitefish were sexually mature by age 4 and all females age 6 and older were sexually mature, but by 1998, about 50% of females were not sexually mature until age 5 and 100% maturity did not occur until after age 10. Causes of the decline in lake whitefish growth in the main basin are not clear. In Lake Michigan, condition and growth of lake whitefish declined as dreissenid mussels proliferated and *Diporeia* populations crashed (Pothoven et al. 2001). As of 1999, declines in *Diporeia* populations in Lake Huron have only been detected in outer Saginaw Bay. Measurement of benthic production has been limited to very few locations outside the bay, most of which are in US waters, making it difficult to assess the effect of lakewide changes in *Diporeia* abundance on lake whitefish growth.

Piscivores

Ambitious salmonine stocking programs had already begun in the Great Lakes in the late 1960s when Berst and Spangler (1973) reviewed the status of Lake Huron's fish community. The initial intentions for introducing Pacific salmon were to control populations of alewife and rainbow smelt and to create a sport fishery (Tody and Tanner 1966). Since 1973, the numbers of planted Pacific salmon, brown trout (*Salmo trutta*), rainbow trout or steelhead, and lake trout expanded. A variety of life stages were planted, including eyed eggs, fry, fingerlings, and yearlings. Annual stocking of all species combined increased from 0.8 million in 1968 to 15.9 million in 1992. The latter figure includes walleye (*Sander vitreus*), which have been stocked since 1978. Management agencies capped predator stocking in 1992, and stocking of chinook salmon was reduced by 20% in 1992 and by another 20% in 1999.

Fig. 4. (*a*) Commercial yield of coregonids (solid area), salmonids (open), percids (cross-hatched), and other species (shaded) from Lake Huron between 1930 and 1999. (*b*) Commercial yield of lake whitefish only.



Lake trout

Berst and Spangler (1973) doubted that economically sound lake trout management could be achieved in Lake Huron even if sea lamprey abundance could be held to low levels. Their pessimistic assessment was based on a belief that lake trout were extremely vulnerable to sea lamprey predation. To resolve the problem of extreme vulnerability, the province of Ontario had already begun stocking splake as an alternative to the late-maturing lake trout.

During the 1990s, vigorous debate over the collapse of lake trout populations centered on the relative importance of sea lamprey predation and overfishing. Some researchers attributed the collapse principally to sea lamprey predation (Berst and Spangler 1973; Coble et al. 1990) and others to overfishing (Eshenroder et al. 1995; Spangler and Peters 1995), while some argued that both the sea lamprey and fishing were important (Hansen 1999). In Lake Huron, the debate focused on the lean form of the lake trout harvested in the main basin in the 1940s. Deepwater forms of lake trout were extirpated by 1925, well before sea lampreys entered the lake (see Sea lamprey section). The role of deep-

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water lake trout in Lake Huron continued to be overlooked when reintroduction of lake trout and splake stocking began in the early 1970s.

By 1974, lake trout were stocked only in the main basin, and there only in Michigan waters. The planting of approximately 1 million lake trout per year has not led to sustainable reproduction. Naturally reproduced lake trout in the main basin were as scarce at the end of the 1990s as they were at the start of that decade. Exactly what inhibits natural reproduction of lake trout is not clear (Eshenroder et al. 1999), but the problems identified by Eshenroder et al. (1995) for the main basin remain unresolved: low stocking levels aggravated by stocking an already inadequate allocation of fish in areas of sparse reproductive habitat, a net migration of fish from Michigan waters into unstocked areas on the Ontario side of the main basin, and excessive mortality from fishing and sea lampreys (also see Sitar et al. 1999). Sea lamprey predation and fishing mortality rates, however, are likely to be lower in the near future than in the 1990s, a result of sea lamprey control efforts on the St. Mary's River and fishery management efforts associated with the 2000 renegotiation of an agreement on Native American treaty rights in US waters. Treatment of the St. Mary's River has already led to a modest reallocation of lake trout stockings to the northern part of the main basin where lake trout spawning habitat is more concentrated (see Sea lamprey and Fisheries sections).

The prospects for rehabilitation of lake trout appear to be better in Georgian Bay where two small populations persisted (Berst and Spangler 1973), in part because sea lampreys were less abundant there (Eshenroder et al. 1995). The genotype stocked in Georgian Bay has changed from splake in the 1970s to a predominance of splake backcrossed to lake trout in the 1980s to a predominance of pure lake trout in the 1990s (Eshenroder et al. 1995). The stronger of two persisting populations in the Bay, the one in Parry Sound (Fig. 1), was augmented with stocked lake trout spawned from adults collected at the same locality. Reid et al. (2001) estimated that the spawning population in 1994–1997 ranged from 16 000 to 29 000 individuals. As the lake trout population increased, sea lamprey marking rates approached zero, reflecting a favorable sea lamprey to lake trout ratio and negligible mortality caused by sea lamprey. In comparison, during 1958, prior to effects of sea lamprey control in the bay that began that year, high marking rates in Parry Sound indicated that sea lamprey attacks were causing an increase in instantaneous mortality rates between 0.32 and 0.58·year^{-1} (Reid et al. 2001). The spawning stock that produced wild recruits was fortified by high stocking rates, but stocking in Parry Sound discontinued after 1997 because the large spawning population was composed mainly of wild fish. The Parry Sound lake trout population is the only Lake Huron population considered to be rehabilitated.

Trends in biomass and consumption by piscivores

Increases in predator stocking rates, rehabilitation of lake trout, and treatment of the St. Mary's River for sea lampreys prompted concerns that increased predator populations could exceed the productive capacity of the open-water prey fish community. Increases in salmon stocking during the 1980s were associated with declines in prey abundance and slower growth of chinook salmon (Fig. 5). The proportion of age-4 chinook salmon, the oldest age in the spawning run, increased from 0.4% from 1974 to 1981 to 15.2% from 1996 to 1999 (J.E. Johnson, unpublished data). Thus, as growth declined, possibly in response to declining alewife abundance, maturation of salmon was delayed. A similar scenario preceded a collapse of the chinook salmon fishery in Lake Michigan (Holey et al. 1998).

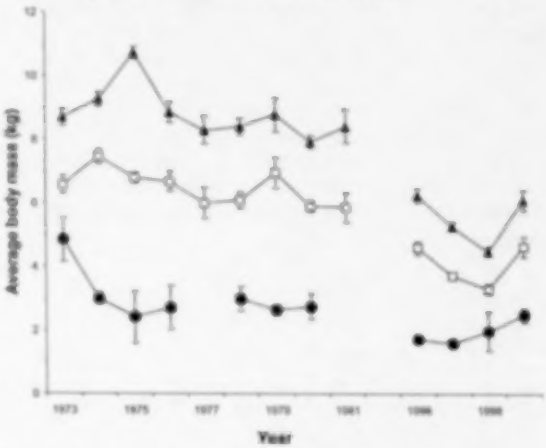

Fig. 5. Average mass and 95% confidence intervals for individual age-1 (circles), age-2 (squares), and age-3 (triangles) mature chinook salmon (*Oncorhynchus tshawytscha*) caught on the AuSable River, western Lake Huron, 1973–1999. Mean masses at each age were significantly different between 1973–1981 and 1996–1999. Two-tailed Mann–Kendall trends tests yielded $S = -29$ and $p = 0.0293$, $S = -54$ and $p = 0.0012$, and $S = -52$ and $p = 0.0019$ for ages 1–3, respectively. Significant Mann–Kendall trend tests indicate a nonrandom pattern generated by systematic trend or temporal correlation in the time series.

To explore whether top predators were overly abundant and to determine how the system has changed since Berst and Spangler's (1973) account, a time when planktivores dominated the fish community, mean predator biomass and consumption of prey in Lake Huron were estimated for the period 1984–1998 (Dobiesz 2003). This exercise was restricted to the main basin because of the availability of data and focuses on four key predators: chinook salmon, lake trout, walleye, and burbot. Other species, coho salmon (*Oncorhynchus kisutch*), brown trout, pink salmon (*Oncorhynchus gorbuscha*), and rainbow trout, have played a less significant role in fish community dynamics.

We used the Mann–Kendall trend test (Kendall 1975) to examine trends in biomass and consumption. The combined biomass of the key predators trended slightly upward ($S = 45$, $p = 0.0294$) during 1984–1998, but the composition of that biomass changed substantially (Fig. 6*a*). Total biomass averaged 10.3 million kg, with average species-specific contributions ranging from 2.1 million kg for burbot to 2.8 million kg for chinook salmon. Lake trout biomass was the only one that declined substantially. Most of this decline occurred in the southern main basin and was attributed primarily to declines in stocking in that region (Sitar et al. 1999). By contrast, chinook salmon biomass increased substantially

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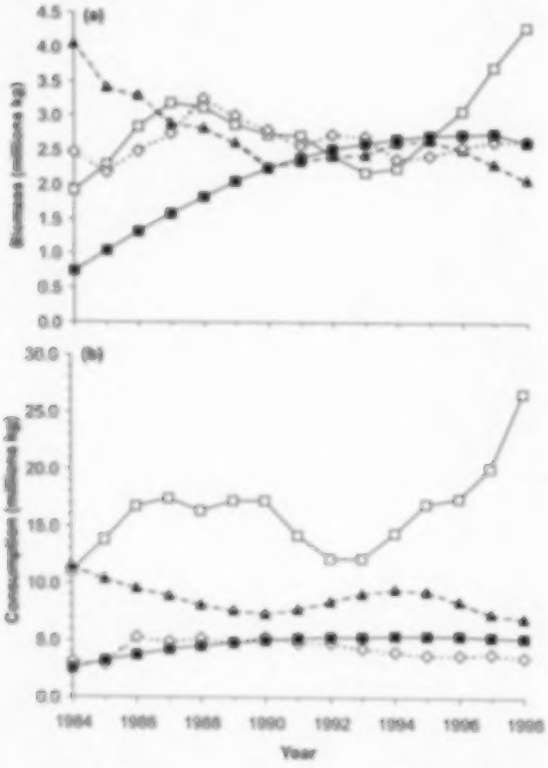
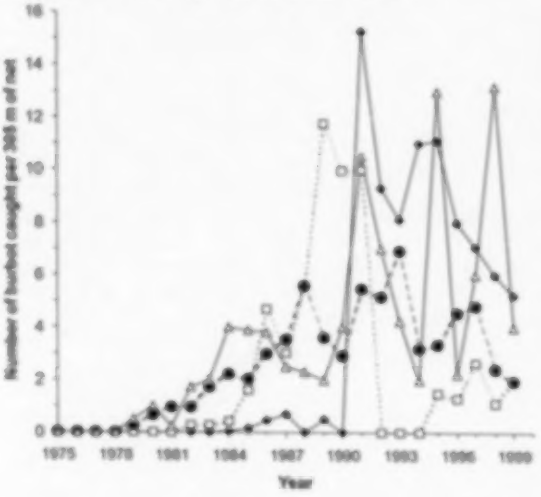
Fig. 6. Estimated (*a*) biomass and (*b*) consumption by the major piscivores chinook salmon (*Oncorhynchus tshawytscha*) (open squares), lake trout (*Salvelinus namaycush*) (triangles), walleye (*Sander vitreus*) (open diamonds), and burbot (*Lota lota*) (closed squares) in the main basin of Lake Huron during 1984–1998 estimated from stock assessment and bioenergetics models (Dobiesz 2003). Two-tailed Mann–Kendall trend tests of biomass yielded $S = 21$ and $p = 0.3223$, $S = -63$ and $p = 0.0022$, $S = -3$ and $p = 0.9212$, and $S = 97$ and $p < 0.0001$ for chinook salmon, lake trout, walleye, and burbot, respectively. Two-tailed Mann–Kendall trends tests of consumption yielded $S = 39$ and $p = 0.0600$, $S = -43$ and $p = 0.0377$, $S = -41$ and $p = 0.0478$, and $S = 85$ and $p < 0.0001$ for chinook salmon, lake trout, walleye, and burbot, respectively. Significant Mann–Kendall trend tests indicate a nonrandom pattern generated by systematic trend or temporal correlation in the time series. Trends for burbot are based on assumed constant recruitment at age 1 with constant natural and fishing mortality and decreasing sea lamprey induced mortality, so these patterns reflect an overall trend and not year-to-year variation.



(Fig. 6*a*). Almost all of this increase was in 1997–1998, which occurred despite declines in mean weight-at-age between 1974–1981 and 1996–1999 (Fig. 5).

Even though burbot mean biomass is relatively low (Fig. 6*a*), historically, burbot were likely an important predator in Lake Huron. Berst and Spangler (1973) noted that the burbot population declined concomitantly with the collapse of the lake trout population, but no data were presented. Until the early 1980s, burbot were rare in Lake Huron assessments but they were taken frequently in recent years

Fig. 7. Number of burbot (*Lota lota*) caught in 305 m of index gill nets set by the Michigan Department of Natural Resources at several sites throughout Lake Huron, 1975–1999, in Georgian Bay (triangles) and the northern (diamonds), central (squares), and southern (circles) regions of the main basin.



(Fig. 7). Although there is no way to compare their current abundance with that of pre-sea lamprey days, this species was consuming a nonnegligible amount of prey biomass by the 1990s (Fig. 7) and is important in the lake's food web (Eshenroder and Burnham-Curtis 1999).

Overall, walleye biomass varied without trend, but the biomass of Saginaw Bay walleyes, which feed in the main basin proper, increased, while the biomass of walleyes in the southern main basin declined (Dobiesz 2003). Except for the recovery of walleye populations in Saginaw Bay (Mrozinski et al. 1991), walleye populations do not appear to have changed much since Berst and Spangler (1973) gave their account. Substantial numbers still migrate from Lake Erie into southern Lake Huron (McParland 1996) and support commercial and angling fisheries. Populations inhabiting the larger rivers along the east shore of the North Channel and Georgian Bay also persist, while those inhabiting the smaller rivers remain depleted (Reckahn and Thurston 1991; Eshenroder 2003).

Lake trout and chinook salmon accounted for 73% of the 34.2 million kg of prey fish consumed on average by all four key piscivores during 1984–1998. Chinook salmon increasingly dominated consumption, with a significant upwards trend during the 1990s ($S = 20$, $p = 0.0476$). Since the increase happened over just a few years, the trend over the entire modeled period was nonsignificant ($S = 39$, $p = 0.06$) (Fig. 6*b*). Most of the increase occurred in the latter years and was caused by increased stocking of chinook salmon during the first half of the 1990s and improved stocking methods (e.g., net pens) during the later half of the 1990s. Already the dominant predator in 1984, chinook salmon became even more abundant, partly at the expense of lake trout, during 1984–1998. In this period, estimated total consumption of prey fish by lake trout declined from a high of 12.2 million kg to 7.6 million kg. During 1984–1998, consumption by walleye and burbot was similar, accounting for 20% of the total annual consumption.

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From 1996 to 1998, when consumption averaged 37.8 million kg, alewives were the predominant prey and comprised 54% of total consumption. Rainbow smelt were next in importance and comprised 28% of total consumption. Lake trout, chinook salmon, and walleyes fed heavily on alewives and rainbow smelt, which comprised 97%, 83%, and 60% of their diets, respectively. In contrast, burbot fed more on invertebrates and sculpins, which accounted for approximately 49% of their diet (Dobiesz 2003).

Cormorants

The double-crested cormorant (*Phalacrocorax auritus*), a piscivorous waterbird, has gained some importance as a fish consumer in Lake Huron (Weseloh et al. 1995). The first confirmed nesting occurred in 1932, and by the 1940s, as many as 3000 breeding pairs resided on Lake Huron (Ludwig and Summer 1997). Egg-shell thinning and other reproductive failures tied to dichlorodiphenyltrichloroethane (DDT) contamination caused populations to plummet by the 1970s. Consequently, Berst and Spangler (1973) did not identify this bird as an important piscivore. Following the DDT ban, cormorants exhibited a spectacular population increase on Lake Huron (Weseloh et al. 1995), from fewer than 1000 active nests in 1980 to about 27 000 nests in the mid-1990s (Ludwig and Summer 1997; Weseloh et al. 2002) and 40 000 nests in 2000 (Weseloh et al. 2002; C. Weseloh, Canadian Wildlife Service, 4905 Dufferin Street, Downsville, ON M3H 5T4, Canada, personal communication; D. Fielder, Michigan Department of Natural Resources, 106 East Fletcher, Alpena, MI 49707, USA, personal communication.). Although the highest density of nests is in the North Channel, cormorants have also expanded their nesting range (Weseloh et al. 2002). By 2000, 38% of nests were around the main basin and the remaining nests were equally divided between the North Channel, including the St. Mary's River, and Georgian Bay.

We estimated that in 2000, cormorants consumed approximately 13.9 million kg of fish, 5.3 million kg of which was consumed in the main basin. Consumption by cormorants in the main basin is equivalent to about 18% of the estimated consumption by key piscivores in the main basin during 1996–1998. These estimates assume that 346 kg were consumed annually by the birds associated with each nest (Madenjian and Gabrey 1995). Although we do not have an estimate of consumption for nonresident (migrant) birds in Lake Huron, migrant birds consumed 19% of the resident total in western Lake Erie. Because cormorant foraging is centered around shore and island colonies, shore-associated fishes such as smallmouth bass (*Micropterus dolomieu*), yellow perch (*Perca flavescens*), walleye, and recently stocked salmonines can figure prominently in diets. Cormorant predation has been a particular concern regarding anglers of yellow perch in the Les Cheneaux Islands region (Diana and Maruca 1997) and some populations of smallmouth bass.

Sea lamprey

Sea lampreys have been at pest levels of abundance in Lake Huron since the 1980s, despite intensive control efforts. Berst and Spangler (1973) implicated the sea lamprey as the principal cause of the impairment of Lake Huron fisheries and advocated a second round of lampricide applications in infested streams. As of 1999, eight rounds involving 620 applications have been made to Lake Huron tributaries (Morse et al. 2003).

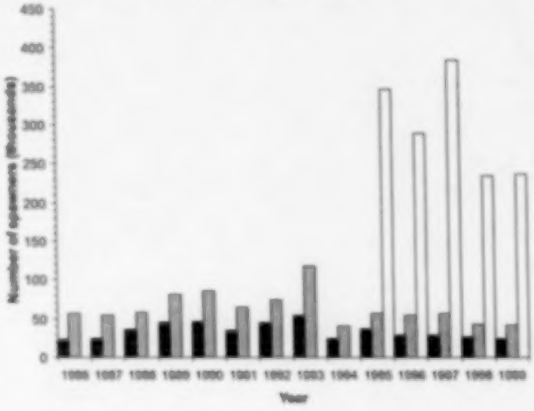

Fig. 8. Numbers of spawning-phase sea lampreys (*Petromyzon marinus*) captured in assessment traps from an average of 13 Lake Huron streams (range 9–16, solid bars), their estimated populations in the Cheboygan, St. Mary's, and Thessalon Rivers from 1986 to 1999 (shaded bars), and the estimated lake population from 1995 to 1999 (open bars).

Juvenile sea lampreys were not abundant when reintroduction of lake trout began in earnest in the main basin in 1973. Although the parasitic (juvenile) population expanded after the first individuals were observed in 1937 (Applegate 1950), numbers declined by as much as 85% from 1949 to 1970 (Schleen et al. 2003). Thus, the juvenile (parasitic) population in the main basin was already reduced in number when the first round of lampricide treatments was completed, but low abundance of juveniles was largely attributable to a dearth of suitable hosts rather than just to reduced survival of stream-inhabiting larvae caused by lampricide treatments. The dynamics of this situation became clearer when sea lamprey numbers surged in the early 1980s (Fig. 8) in association with a modest recovery of bloater, a preferred prey of young juveniles (Eshenroder et al. 1995).

The only large population of untreated larvae known in Lake Huron was in the St. Mary's River, a wide connecting channel that drains Lake Superior. Although sea lamprey larvae infested the river as early as 1962 (Schleen et al. 2003), two factors weighed against a treatment: its great discharge (mean 2100 $m^3 \cdot s^{-1}$) made the efficacy of a conventional and potentially costly treatment problematical and the extent of the larval population was unknown. By 1996, this situation was rectified when the St. Mary's population of larvae was estimated at 5.2 million individuals based on a multiyear survey (Fodale et al. 2003).

Treatment of the St. Mary's River with the commonly used lampricide TFM was ruled out because maintaining a lethal dose at the bottom of the water column was problematic. Indeed, the amount of TFM needed for a conventional treatment of the river was estimated at 2.5–6.5 times the average annual use in all of the Great Lakes (Schleen et al. 2003). An alternative approach using Baylucide embedded in time-release granules was employed in 1998 and 1999 to

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treat 860 ha of the riverbed, estimated to harbor 45% of the larval population (Schleen et al. 2003). This treatment was intended to enhance sterile-male release and adult trapping control programs. Combined, these methods were projected to reduce the number of juvenile sea lampreys in Lake Huron by 85% (Morse et al. 2003). The high level of parasitism in the main basin before the Baylucide treatment was seen as so onerous that stocking of lake trout in northern waters was halted in 1993 — stocking resumed prior to the treatments in the St. Mary's River, in anticipation of reduced sea lamprey predation.

The outcome of the recent control efforts on the St. Mary's River remains to be determined. The success of lake trout rehabilitation in the main basin and the North Channel is assumed to be tied to successful sea lamprey control. In these areas, a mid-1990s population in excess of 0.5 million was believed to limit the reestablishment of a viable lake trout population (Eshenroder et al. 1995). By contrast, prospects for lake trout rehabilitation are much better in Georgian Bay. Sea lampreys were slower to colonize the bay and control has been more effective (Eshenroder et al. 1995), and wild lake trout are already abundant in some areas. Although sea lampreys may have the upper hand in most of Lake Huron, ongoing experimentation with pheromone-based control methods (Li et al. 2002) will hopefully improve suppression.

Fisheries

Berst and Spangler (1973) advocated a greater role for overfishing than for sea lampreys in restructuring the lake's fish community. Spangler and Peters (1995) held that overfishing was pervasive by the late 1800s and suggested that landings of lake trout held up for as long as they did because the populations were being fished-up sequentially. The fishing-up process accelerated with the introduction of the steam tug, first used in Michigan waters in 1860, which allowed the fishery to expand to offshore waters. Spangler and Peters (1995) were not clear whether offshore fishing in any of the basins before the twentieth century represented growth overfishing (harvesting below the optimum size) or recruitment overfishing. Lake trout landings held up for a remarkably long time, until the 1930s, considering how long the offshore populations were accessible to the fishery.

During 1970–1999, the regulatory framework and gears used in the commercial fisheries underwent profound changes, and a more sophisticated offshore recreational fishery targeting Pacific salmon and lake trout developed. The traditional regulatory framework (offshore fisheries were essentially commercial with open entry and equal access to fishing grounds) was still in place when Berst and Spangler (1973) wrote their overview. Shortly after introducing salmon in the late 1960s, the State of Michigan initiated major regulatory changes in its commercial fisheries that partly reflected their new emphasis on recreational fishing. The most important modifications were the closing of all waters except Saginaw Bay to large-mesh gill nets, typically used to take lake whitefish and lake trout, banning the catch of deepwater ciscoes and walleyes, and issuing licenses only to those who could demonstrate a livelihood from fishing (Brege and Kevern 1978). In 1984, the Province of Ontario also made major regulatory changes that entailed a system of transferable quotas (Brown et al. 1999).

The reduction in commercial fishing and associated decrease in fishing mortality on lake trout were short lived. Commercial fishing under treaty rights began first in Michigan waters and then in Ontario waters, and recreational fisheries began to take substantial numbers of lake trout. Treaty fishing led to increased commercial landings during the late 1970s and 1980s (Fig. 4*b*) as more gear was being fished, especially in Michigan, although these larger yields would not have been possible without the rebounding lake whitefish populations. During the 1960s, lake whitefish comprised 18% of the total landings and by 1999 this figure increased to 80% (Fig. 4*a*). The use of large-mesh gill nets (10.16–30.48 cm), which Michigan and Ontario wanted to minimize to reduce bycatch of lake trout, also increased during this period (Brown et al. 1999). Of all of the fishing gears employed, lake whitefish gill nets have undergone the most improvement. Monofilament twine of only 0.17-mm diameter has replaced multifilament twine of 0.27 mm, and nets have deepened by a factor of 3 (Brown et al. 1999).

Following two negotiated settlements (United States of America and four Native American bands v. State of Michigan et al. 1985; United States of America and eight Native American bands v. State of Michigan et al. 2000), commercial fishing in Michigan's northern waters became restricted to tribal members and was managed under tribal regulations. A state-managed recreational fishery shares the lake trout resource under agreed-upon mortality targets and allocations of yield. Under the 1985 agreement (United States of America and four Native American bands v. State of Michigan et al. 1985), target mortality rates for lake trout were not put in place for the northernmost Michigan waters of the main basin, except for a refuge where commercial fishing and recreational take of lake trout were not allowed (Fig. 1). Lake trout rehabilitation was deferred in these waters, which contained some of the historically most productive lake trout spawning grounds (Eshenroder et al. 1995). The 2000 agreement (United States of America and eight Native American bands v. State of Michigan et al. 2000) established target mortality rates for lake trout and an approach for encouraging a change from gill nets to trap nets. A similar management arrangement between Ontario First Nations and management agencies does not exist (Brown et al. 1999).

Assessment of recreational fishing effort and harvest began during the mid-1980s. Of the three main recreational fisheries, the offshore salmonine and nearshore warm- and cool-water fisheries have been at least partially assessed in most years, whereas the river fishery for salmonines has been essentially unmonitored in a number of years. An extended time series for the in-lake fisheries is available for the main basin but not for Georgian Bay or the North Channel. Recreational effort in the combined offshore and warm- and cool-water recreational fisheries (in-lake fishing) of the main basin was at a peak of over 4 million angler hours in 1986, the first year for which there is an overall estimate, and subsequently declined and stabilized during the 1990s at approximately 3 million angler hours per year (Fig. 9*a*). Michigan anglers accounted for most of this fishing activity. Main basin in-lake recreational fishing effort has been almost equally divided between salmonine and percid fisher-

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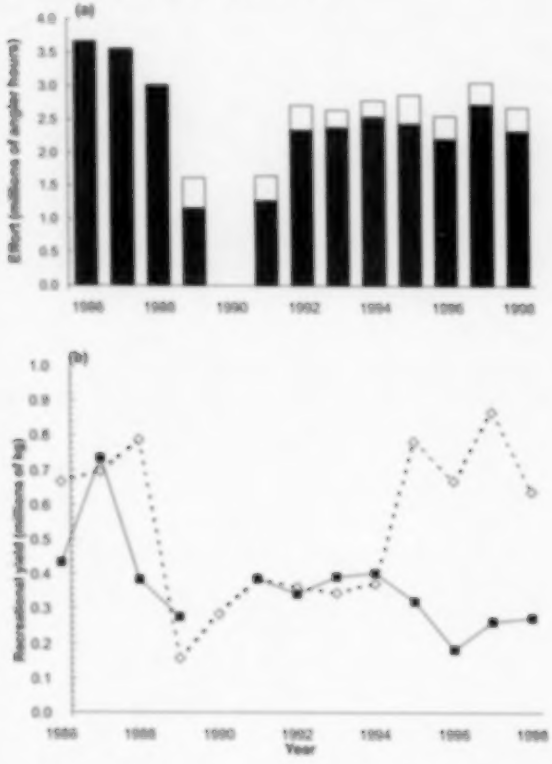
Fig. 9. (*a*) Recreational fishing effort in Canadian waters (open bars) and US waters (solid). (*b*) Recreational yield of salmonines (diamonds) and nonsalmonines (squares). Data derived from creel surveys conducted by Michigan Department of Natural Resources and the Ontario Ministry of Natural Resources in the main basin of Lake Huron, 1986–1998.



ies, although during the 1990s, the emphasis in Ontario waters shifted from other species to salmonines (Mohr and Nichol 1998). In the main basin (excluding rivers), percids far exceed salmonines in the numbers harvested (but not in yield), reflecting the high catch rates of smaller-sized yellow perch (Bence and Smith 1999). However, in the late 1990s, the contribution of salmonines increased, reflecting a decrease in the yield of percids and an increase in the yield of salmonines (Fig. 9*b*). The recreational yield for Georgian Bay and the North Channel combined was roughly equal to the main basin yield in 1995 and consisted primarily of inshore fishes: yellow perch, walleye, and smallmouth bass.

Yield can only be compared between the angling and commercial fisheries for the whole lake for 1995, a year when anglers took just over 2 million kg of fish and the commercial fishery took just under 6 million kg. Angler yield that year was equally divided between the main basin and the North Channel and Georgian Bay combined. In the late 1990s, annual recreational yield in the main basin continued to average near the 1 million kg taken in 1995 (Fig. 9*b*).

Contaminants

Concentrations of contaminants in the waters and fishes of Lake Huron declined during 1970–1999. Berst and Spangler (1973) cautioned that chlorinated hydrocarbons and toxic metals under the right conditions might jeopardize the survival of lake whitefish, ciscoes, and lake trout. Since that time, bans on the use of major pollutants such as DDT and polychlorinated biphenyls contributed to declines in concentrations of both chemicals (Stevens and Neilson 1989). Ongoing monitoring and shorter term studies have shown that concentrations in Lake Huron fish from both US and Canadian waters are now lower than they were in the 1970s, although the decline has been slower than expected and may reflect food web changes (Frank et al. 1978; De Vault et al. 1996; Scheider et al. 1998). Lake trout are the most sensitive fish tested, but ambient levels of polychlorinated biphenyls (a toxin of particular concern) in lake trout from all of the Great Lakes are below levels associated with acute effects (Fitzsimons 1995). Consequently, recent research on toxic substances is shifting to chronic effects and to interactions between toxic chemicals and other maladies (Eshenroder et al. 1999). Despite reductions in contaminant loading, fish consumption advisories continue to be issued for certain fishes.

Exotics

Introductions with the potential to cause lake-wide impacts in the Great Lakes can be viewed as having arrived in two waves. The first wave arrived during the 1920s–1930s, well before SCOL-1 (Berst and Spangler 1973), and consisted of rainbow smelt, alewife, and sea lamprey. The second, more recent wave, entering via ballast water from ocean-going ships, was predominantly invertebrates: the spiny water flea (*Bythotrephes longimanas*), dreissenid mussels (*D. polymorpha* and *D. bugensis*), the fishhook water flea (*Cercopagis pengoi*), and the round goby (*Neogobius melanostomus*) (Shuter and Mason 2001).

Community effects of first-wave invaders are still not completely understood (Eshenroder and Burnham-Curtis 1999) even though the second wave is well established. Moreover, first-wave invaders typically exert effects at higher trophic levels, more readily analyzed with existing fishery models, whereas second-wave invertebrates are expected to impact lower levels, not readily evaluated by conventional fishery models (Shuter and Mason 2001). New invaders will likely also alter, mask, or confound the effects of earlier invaders, making catching up with system changes difficult. Thus, the issue of introductions, already complex at the time of SCOL-1, has become even less tractable because sampling of lower trophic levels, especially in Lake Huron, is sparser than it is for fish.

Aquaculture

The commercial culture of fish in cages or pens expanded substantially on Lake Huron in the 1990s. Since 1980, the number of cages increased from 0 to over 100 producing approximately 7.0 million kg of rainbow trout annually. Escapement of cultured fish in the North Channel may range from 7000 to 10 000 fish each year. Cage culture is an emerging concern because such fish can be vectors for disease and escapees could breed with wild rainbow trout.

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Prognosis

Prospects for rehabilitation of the native salmonid communities of Lake Huron appear far brighter to us than they did to Berst and Spangler (1972, 1973). Our perceptions reflect the recovery of lake whitefish populations, reestablishment of substantial populations of top-level predators, and progress toward control of sea lamprey and limitation of fishing mortality. Nevertheless, maintaining what has heretofore been accomplished will require intensive management, and further progress in rehabilitating native species is uncertain.

We see two scenarios for Lake Huron's fish community — which one prevails depends on whether lake trout become self-sustaining. Assuming no surprises such as another inimical introduction, if lake trout recover and their population is allowed to expand, we anticipate that they would eventually replace hatcheries as drivers of the system, as in Lake Superior (Hansen et al. 1995). Under this scenario, we would expect a substantial recovery of yellow perch (beyond the large bays), walleye, lake herring, and deepwater ciscoes, whose fry, including those of two extirpated species, entrain regularly into Lake Huron via the St. Mary's River. Salmon fisheries would scale back but remain more prominent than they are in Lake Superior. In our second scenario, lake trout rehabilitation largely fails. Periodic dieoffs of alewives and salmon occur and major concerns become preventing loss of fitness in hatchery-origin populations and promoting naturalization of Pacific salmon. Room obviously exists between these scenarios, for instance, a full lake trout recovery in Georgian Bay, where it now has a head start, and no recovery in the main basin — an intriguing situation that would make vivid the differences between community types in the same lake.

Which of these scenarios will occur is unpredictable, in part because of our uncertain knowledge of how Lake Huron functions. We can make educated guesses on how fishery management actions, and other "forcing functions", will influence the relative likelihood of these alternatives. The forcing functions that seem to us most influential are related to top-down actions of fishery management. In particular, the outcome is likely to be influenced by the success of sea lamprey control, limitation of harvest (particularly of lake trout), and plantings of fish. In essence, we believe that rehabilitation of self-sustaining stocks of lake trout will require (*i*) development of a large, diverse population of lake trout spawners and (*ii*) maintaining sufficient numbers of predators so that alewife and rainbow smelt are maintained at low densities. In addition, an at least partial recovery of ciscoes will require limits on fishing them.

Development of a large population of spawning lake trout will require holding lake trout mortality rates to low levels. Control of fishing and sea lamprey is critical here. The need to suppress sea lampreys was identified long ago by Berst and Spangler (1973). In large part, we do not share their pessimism about lake trout restoration in the face of sea lampreys because self-sustaining populations of lake trout were reestablished in Lake Superior subsequent to successful sea lamprey control. Similar reductions in mortality caused by sea lamprey were not sustained in the main basin of Lake Huron because of the large number of parasitic-phase sea lamprey entering the lake from the previously uncontrolled St. Mary's River. Sea lamprey control on this river intensified in the late 1990s, and an 85% reduction in sea lamprey induced mortality on lake trout in the main basin was projected (Schleen et al. 2003). If this projection is met, sea lamprey induced mortality on lake trout in the main basin of Lake Huron will be comparable with levels in Lake Superior. If intensified control is unsuccessful, we doubt whether widespread rehabilitation of lake trout is possible, particularly in the main basin. Sea lampreys from the St. Mary's River play a lesser role in Georgian Bay; thus, some further expansion of the self-sustaining population of lake trout in the bay seems possible without successful control on the St. Mary's River.

Fishery management on Lake Huron currently limits harvest and restricts fishing mortality on most at-risk species, including lake trout. We emphasize that fishery removals reduce the spawning biomass that is potentially obtainable from each stocked lake trout (Sitar et al. 1999) — there is no harvestable surplus that can be removed without a cost to rehabilitation. On Lake Superior, where lake trout have recovered, fishing pressure has generally been lower than on Lake Huron. In that area of Georgian Bay where a population of lake trout is recovering, fishing is highly restricted (Reid et al. 2001). Thus, there will continue to be a trade-off between improved chances of rehabilitation and current fishery harvest.

Although we believe that fishery management is currently sustainable for most fishes except lake trout, we have concerns regarding current harvest policies for bloater. These same concerns would apply to other deepwater ciscoes (chubs) if they were to reestablish in Lake Huron. Bloater fishing is managed typically through quotas based on recent yields. Cycles in population size and sex ratio, not precipitated by overfishing, can create a situation where even seemingly low levels of fishing, in fact, become too high.

We believe that the prospects for our first scenario, which involves rehabilitation of lake trout, would be vastly improved were the plantings more diverse phenotypically, greater in number, and concentrated in regions where spawning habitat is most plentiful. Recovery of a self-sustaining population of lake trout in Georgian Bay followed a period of stocking that exceeded levels recommended by Ebener (1998). Stocking levels in the remainder of Lake Huron have generally been lower than recommended by Ebener (1998), and stocking often has not been targeted on the best spawning habitat, which is most plentiful in northern waters (Eshenroder et al. 1995). Recovery of self-sustaining populations of lake trout in Lake Superior, too, followed high levels of stocking. The resulting spawning populations were larger than those seen well before the collapse of historical populations (Wilberg et al. 2003). The diversity of lake trout in Lake Superior during rehabilitation was also much greater than it has been in Lake Huron, as deepwater forms of lake trout (siscowets and humpers) remained reasonably abundant in Lake Superior during rehabilitation (Hansen et al. 1995). The historical populations of lake trout in Lake Huron were also phenotypically diverse (Eshenroder et al. 1995), and the current attempt to replace them with only the lean (inshore) form may be self-defeating (Eshenroder et al. 1999). We

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urge inclusion of deepwater forms of lake trout as part of a stocking strategy aimed at recolonizing both inshore and offshore waters.

We suspect that suppression of exotic planktivores, particularly alewife, by chinook salmon primarily, will play an important role in determining whether lake trout restoration occurs. Alewife is a known predator of lake trout larvae (Krueger et al. 1995). Furthermore, lake trout that feed heavily on alewife suffer from thiamine deficiency, resulting in high mortality of their fry from early mortality syndrome (McDonald et al. 1998). Low abundances of alewife may promote restoration of other species. The evidence is compelling that alewife as well as rainbow smelt suppress the recruitment of important native species: ciscoes, lake trout, burbot, walleye, yellow perch, and deepwater sculpins (reviewed in Eshenroder and Burnham-Curtis 1999). Current and anticipated levels of lake trout stocking alone will not exert the predation pressure necessary to drive alewife and rainbow smelt populations to more tolerable densities. Chinook salmon clearly exert substantial predation pressure on exotic planktivores in Lake Huron as they have in other lakes. Recent reductions in the abundance and survival of alewives and rainbow smelt (J. Schaffer, USGS Great Lakes Science Center, 1451 Green Road, Ann Arbor, MI 48105, USA, personal communication; Dobiesz 2003) are likely a consequence, at least partly, of high predatory demand by piscivores.

Managing for recovery of lake trout as a dominant top predator, as called for in the lake's fish community objectives (DesJardine et al. 1995), is intertwined with the concern that densities of alewife will become too low to support a substantial recreational fishery for salmon. Recent observations of slower growth by chinook salmon combined with evidence they consume a substantial proportion of available alewife (Dobiesz 2003) led managers in 1999 to reduce chinook salmon stocking to avoid a collapse of the salmon fishery as occurred in Lake Michigan during the 1980s. These cuts may have been detrimental to lake trout rehabilitation. We suspect that no balance point exists where exotic planktivores are abundant enough to support a salmon fishery, like that of the 1990s, but not too abundant so as to interfere with a widespread recovery of lake trout populations. This conundrum presents a dilemma to fishery managers. While managers continue to wrestle with this thorny issue, the "stocking lever" may no longer function as in the past. Preliminary results from a marking study to assess wild production of chinook salmon suggest that most salmon in the lake are wild born rather than hatchery reared (J.E. Johnson, unpublished data). This observation may represent a transition in the system that can facilitate recovery of lake trout.

Other forcing functions, besides top-down actions, are less likely, in our opinion, to determine the overall trajectory of the lake's fish community. King et al. (1997) found a detectable warming signal at South Bay, indicating that Lake Huron's fish community is probably already affected by climate change. A reduction in the production of juvenile salmonines in streams in response to warming (Meisner et al. 1987) could play a role in shaping the fish community, if it were to occur prior to reestablishment of large self-sustaining populations of lake trout, which presumably would by themselves suppress alewife populations. Warming may also have strong affects on fish community dynamics in shallow nearshore areas and bays by reducing the growth and survival of cold-water fishes while improving them for warmwater fishes. Although alewife is near the lower end of its winter thermal tolerance in the Great Lakes (O'Gorman et al. 2004), warming may not enhance its productivity. Dieoffs may occur more often in association with cold springs and (or) winters because severe weather events are predicted to increase with changes in global climate. We suspect that Lake Huron, given its large size and extensive deep water, will remain a suitable habitat for cold-water fishes such as lake trout.

We doubt that changes in nutrient or contaminant inputs will greatly influence the future trajectory of the salmonid fish community and predict that, among the Great Lakes, Lake Huron will likely remain closest to Lake Superior in being least impacted by cultural eutrophication. Berst and Spangler (1972) reported that the limnology of the lake had changed little since the 1800s, except for areas near centers of human activity, particularly inner Saginaw Bay. We found that the offshore waters have changed little in terms of enrichment in the three decades since SCOL-1 except for an increase in nitrate plus nitrite and declining contaminant concentrations. Although some areas, primarily in Ontario waters, may see increases in eutrophication resulting from increased cage culture and hog farming, these influences should be localized and nearshore.

Our prognoses regarding the future direction of the Lake Huron fish community are contingent on the basic structure of the system remaining largely as it is now and on the supposition that our understanding of the current system is not fatally flawed. If fishery scientists had made predictions regarding the future of the lake's fish community prior to the invasion of the sea lamprey and alewife, their predictions would have considerably missed the mark. Both dreissenids and exotic predatory cladocerans (*Bythotrephes* and *Cercopagis*) may alter the future food web in ways that have important and unexpected consequences for fish community structure and fishery production. We suspect that a further proliferation of dreissenids will cause additional declines of *Diporeia* populations in Lake Huron. *Diporeia* populations declined in outer Saginaw Bay in association with mussel colonization, and dreissenids are suspected of causing widespread declines of *Diporeia* populations in Lakes Ontario (Mills et al. 2003) and Michigan (Madenjian et al. 2002). In these two lakes, diet shifts and reduced growth occurred in a variety of fishes: rainbow smelt, lake whitefish, young lake trout, and older alewife. We expect similar changes in fish production in Lake Huron, but we are not predicting that such changes will preclude or enhance the recovery of self-sustaining lake trout populations. The lake whitefish fishery, however, appears to be imperiled now by food web changes even though populations remain abundant. Wholesalers are rejecting or discounting the lean, slow-growing fish from the main basin. If the slow growth and poor condition turn out to be a permanent change related to an as yet unconfirmed decline in *Diporeia*, the decrease in useable yield and its value on the market could be ruinous for the fishery. Further, exotic predacious zooplankters may be responsible for a

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compositional shift of zooplankton, especially cladocerans, impacting larval fish survival (Lehman 1991; Laxson et al. 2003). We are not predicting that dreissenids and exotic predacious cladocerans will cause fish community succession, but the future impacts of these invertebrates are an area of great uncertainty. Likewise, the threat from new exotic species from the Ponto-Caspian region and elsewhere is difficult to overstate (Ricciardi and MacIsaac 2000). All of the progress that has gone into restoring the lake's fisheries and our understanding of the system is jeopardized by inadequate regulation of the shipping industry.

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